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SEVERAL ADDITIONAL PHYCOMYCETES SUBSISTING ON NEMATODES AND AMOEBAE

CHARLES DRECHSLER[1]

(WITH 4 FIGURES)

THE NEMATODE-CAPTURING PHYCOMYCETE WITH PYTHIUM-LIKE CHLAMYDOSPORES

In a brief summary published 12 years ago (**7**: p. 269, *fig. 15C, 15D;* p. 270, lines 7–19) a fungus was recorded that had been found capturing nematodes by means of adhesive material secreted by its unseptate hyphae; the same hyphae later giving rise to globose chlamydospores which with respect to their frequently intercalary position as well as with respect to size and shape strongly resembled the chlamydospores or sporangia of many species of *Pythium*, including the several species so widely familiar in causation of damping-off. The fungus soon afterwards was discussed in regard to its manner of capturing prey (**8**: p. 142, 143), and subsequently (**11**: p. 211) was mentioned as appearing, from similarities of mycelium and predaceous habit, closely related to the conidial phycomycete I then described as *Stylopage hadra*. Its resemblance in vegetative development and predaceous habit to both *S. hadra* and *S. leiohypha* Drechsl. (**12**) was pointed out in a more recent paper (**19**: 248–249) where also

[1] Pathologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture.

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its manner of reproduction was brought into the family Zoopagaceae through the erection of an additional genus, *Cystopage*, on an apparently closely related nematode-capturing form, *C. lateralis* Drechsl., whose consistently lateral chlamydospores differ rather markedly from those of any familiar oomycetous species. Still lacking a binomial, the *Pythium*-like fungus of more ambiguous morphology could be mentioned in a recent review only as an unnamed phycomycete (**21**: p. 276, 290). In supplying a name, now rather belatedly, occasion is taken to amplify the meager characterization previously given.

The fungus appears to be abundant on decaying vegetable materials in the region adjacent to Washington, D. C.; its development having been noted year after year in Petri plates of soft maizemeal agar planted with leaf mold or discolored roots collected near Beltsville, Md., in Arlington, Va., and near Fairfax, Va. Since it has come to light especially often in cultures prepared during the months of April, September, and October, from freshly collected materials, there is reason to presume that in nature, as in the laboratory, it flourishes best under cool, somewhat wet conditions, and that at the higher temperatures of summer its activity declines earlier than the activity, in general, of the nematode-capturing hyphomycetes. Its hyphae, like those of other fungi of similar biological habit, do not grow out from plantings of decaying material into an underlying agar substratum until eelworms have multiplied and are infesting the culture in some number. Once they have made their appearance they extend themselves sparsely through the culture, the individual filaments pursuing courses, which if less conspicuously straightforward than those of *Cystopage lateralis*, are yet little given to pronounced deviation. As soon as they have begun pushing their way into the transparent agar, the hyphae can be observed capturing the eelworms whose presence apparently evoked their development. Before long, where suitable prey, as, for example, *Plectus parvus* Bastian, abounds, enormous numbers of animals may often be seen vainly struggling to escape, or following their disablement, undergoing expropriation of their contents (FIG. 1, *A–E*). Capture is effected, as in *C. lateralis*, *Stylopage hadra*, and *S. leiohypha*, through adhesion to glutinous

material which when freshly secreted appears clear and virtually colorless but later becomes golden yellow; the change in respect to coloration being accompanied by a change from a softly plastic to a firm consistency. As in the other three nematode-capturing zoopagaceous forms and, for that matter, as also in the many nematode-capturing hyphomycetes that utilize adhesive material, the localized masses of sticky secretion can be seen only after an eelworm has been taken, and then only on the portions of hypha that are, or have been, in contact with the animal. From such experience as has been gained so far neither the present fungus nor any other fungus specially adapted for capture of nematodes would seem to secrete beforehand adhesive material in masses visible to ordinary microscopical inspection; though, as was intimated earlier (**8**), the violent withdrawal of eelworms when brushing against the predaceous networks or the stalked knob-cells of various nematode-capturing hyphomycetes suggests that some modification of the hyphal surface, vividly perceptible to animals threatened by it, may be present even when the microscope fails to reveal any cause for alarmed behavior. It is true that *Arthrobotrys entomopaga* Drechsl. (**22**), which now and then captures nematodes in some number, secretes adhesive material copiously beforehand, but there can be no question that the predaceous apparatus of this hyphomycete is primarily adapted for capture of springtails; so that the closer analogy to the trapping devices of the sundews or more especially of the carnivorous phanerogamic genera *Byblis* and *Drosophyllum* may be held to reflect the rather different requirements for capturing insect prey.

While many captured nematodes are fastened to a mycelial filament in only a single place (FIG. 1, *A*, *B*, *C*, *E*), some are fastened in 2 places (FIG. 1, *D*), and others in no less than 3 places. In any case when the individual captive has become quiescent, presumably from exhaustion, its integument is penetrated by an infective process extended from the hypha through the cushion of adhesive material. After the animal's protective layer has been breached, the infective process gives off several assimilative branches often hardly more than half as wide as the external filament. These branches grow lengthwise through the fleshy interior, bringing about globulose degeneration of musculature

and organs in their advance. The firm tissues of the oesophagus and valve resist destruction somewhat better than the softer parts (FIG. 1, *C*, *D*, *E*), but before long these likewise disintegrate. In a short time the globuliferous degeneration products are absorbed with such completeness that nothing of the animal remains visible except the integument, and, in male specimens, the spicula. Thereupon the assimilative branches also become evacuated, by movement of their protoplasmic contents backward into the parent hypha; their empty membranes, like the host integument, soon collapse and disappear from view, leaving only the persistent lump of yellow adhesive material, together, perhaps, with some portions of hyphal envelope, to indicate a concluded instance of predaceous action.

Production of chlamydospores in Petri plate cultures often begins about 8 or 10 days after vegetative development has become noticeable, and may therefore proceed simultaneously with vegetative development if the supply of living prey is replenished through active multiplication of suitable nematodes; though as a rule capture of eelworms will then have greatly diminished in frequency. Formation of a chlamydospore ordinarily is accomplished by withdrawal of protoplasmic contents from the adjacent portions of mycelial hypha; the progressive migration of granular material resulting in a succession of retaining walls spaced at intervals of 5 to 50 μ (FIG. 1, *F–Z*). While generally of subspherical shape, the chlamydospores may in their definitive condition include a short cylindrical part at either end (FIG. 1, *F*), or may consist of two globose parts connected by a living portion of outwardly unmodified hypha (FIG. 1, *G*, *a*, *b*). Aside from axial prolongations, the subspherical shape of the chlamydospores is often modified in some degree by the presence of lateral diverticulations, which frequently are found empty (FIG. 1, *N*, *S*, *T*, *U*), yet sometimes remain filled with protoplasm (FIG. 1, *V*, *P*). Occasionally a chlamydospore may bear a sigillate lump of yellow adhesive material with membranous vestiges of a centrally perforating branch, or, more rarely, may bear two such lumps (FIG. 1, *I*). Manifestly these lumps are entirely similar to those on evacuated hyphae (FIG. 1, *G*, *H*, *I*, *S*, *T*, *U*) and must likewise be interpreted as recording the capture and destruction

of a nematode; the predaceous action, in most instances, probably having been completed, or at least well started, before the development of the chlamydospore began.

The position of the chlamydospores relative to the hyphae bearing them, while hardly to be regarded as a feature of much fundamental importance, yet provides the most convenient diagnostic character of the fungus under consideration. In *Cystopage lateralis*, the only congeneric form known to prey on nematodes, the chlamydospores are invariably formed laterally; whereas in the present species they are more often intercalary (FIG. 1, *F–W*) than lateral (FIG. 1, *X–Z*), though lateral development is apparently never absent here, and in some cultures may even become rather frequent. With the difference in relationship to the parent hypha is associated an appreciable difference in shape; the pouch-like and lobate types of chlamydospores abundant in cultures of *C. lateralis* being only rarely approximated in the present fungus. Further, the two fungi seem to differ in geographical distribution. *C. lateralis* has been found in nearly all collections of leaf mold taken from deciduous woods in northern Wisconsin, but has not been obtained from any of the more numerous collections of leaf mold and decaying roots taken from deciduous woods near Washington, D. C., during the last ten years. The present fungus, on the other hand, has been found represented as meagerly in material from Wisconsin as it has been found represented abundantly in material originating near the District of Columbia. In naming it, however, an epithet contrasting with "lateralis" appears less disadvantageous than any term that might be suggested by the meager distributional information now available.

Cystopage intercalaris sp. nov.

Mycelium sparsum; hyphis continuis, incoloratis, plerumque 3–5.5 μ crassis, saepe plus minusve recta procurrentibus, vermiculos nematoideos glutino primum incolorato mox flavo tenentibus, integumentum cujusque animalis capti perforantibus, ramulos assumentes vulgo 2–3 μ crassos intus evolventibus qui carnem exhauriunt; chlamydosporis saepius intercalaribus sed quandoque a latere hyphae mycelii oriundis, flavidis, vulgo globosis vel elongato-ellipsoideis, plerumque 18–35 μ longis, 15–30 μ crassis.

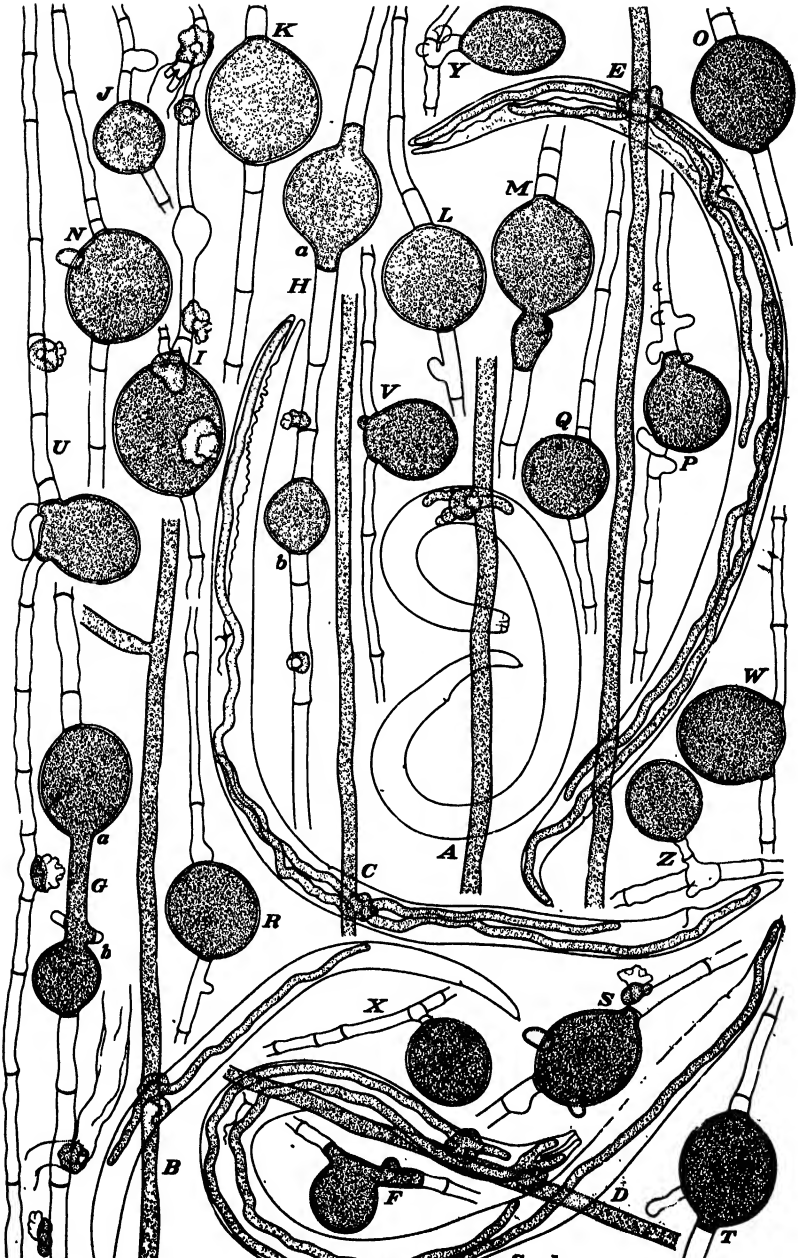

FIG. 1. *Cystopage intercalaris.*

Vermiculos nematodeos diversos usque 500 μ longos capiens consumensque habitat in humo silvestri et radicibus putrescentibus prope Beltsville, Maryland, in Arlington, Virginia, et prope Fairfax, Virginia.

Mycelium sparse; hyphae continuous, colorless, mostly 3 to 5.5 μ wide, by means of an adhesive secretion at first colorless but later becoming golden yellow capturing nematodes, then penetrating the integument of each captive with an infective branch that gives rise within to assimilative filaments, commonly 2 to 3 μ wide, which appropriate the fleshy contents. Chlamydospores usually distinctly yellowish, commonly subspherical or elongate ellipsoidal, mostly 18 to 35 μ long and 15 to 30 μ in greatest width, frequently either mesially or laterally intercalary, and somewhat less often occurring laterally either from lateral development or from development in terminal or subterminal positions in short hyphal branches.

Capturing nematodes up to 500 μ in length, referable to *Acrobeloides*, *Cephalobus*, *Plectus*, *Rhabditis*, and other genera, it occurs abundantly in leaf mold and decaying roots near Beltsville, Md., near Fairfax, Va., and in Arlington, Va.

A SEXUAL STAGE POSSIBLY BELONGING TO CYSTOPAGE INTERCALARIS

In an earlier account (**11**: p. 211, lines 11–18) I made mention of a nematode-capturing phycomycete that had been observed in its sexual reproductive stage. The fungus to which reference was made came to light early in January, 1934, in a maizemeal-agar culture planted 35 days before with several pinches of leaf mold originating from deciduous woods in Arlington, Va. Although predaceous activity had virtually come to an end, apparently because of the small number and sluggish behavior of the surviving nematodes, numerous empty integuments, many of them with an outline and with annulations suggestive of *Acrobeloides bütschlii* (DeMan) Thorne, were found attached to sigillate masses of yellow adhesive material that studded the unseptate, sparsely branched mycelial filaments (FIG. 2, *A*). Each sigillate mass showed clearly a central perforation, and often in addition, membranous vestiges of a haustorial system; wherefore it was evident that numerous eelworms had somewhat earlier been captured and depleted of their fleshy contents.

The entire mycelium of the fungus was looked over carefully for conidiophores, conidia, and chlamydospores, but no asexual reproductive structures could be discovered anywhere. As the mycelial hyphae measured 2.5 to 4 μ in width, they would seem to have been slightly coarser than those of *Stylopage leiohypha*, and slightly more delicate than those of *S. hadra*, *Cystopage lateralis*, or *C. intercalaris;* the dimensional difference in either direction being, however, too small to permit, in itself, recognition of a separate species. Identity with *C. lateralis* appears almost certainly excluded, since that form has not hitherto been seen in cultures prepared with leaf mold from the region surrounding Washington, D. C. Absence of bulbous hyphal protuberances at the places where nematodes were attached cannot be considered to exclude possible identity with *S. hadra*, for when developing on soft agar substrata *S. hadra* often fails to produce such protuberances. Accordingly the predaceous mycelium may belong to *S. hadra*, or with perhaps slightly greater probability to either *S. leiohypha* or *C. intercalaris;* or, again, it may represent a species whose asexual reproductive phase has as yet not come under observation.

Its sexual reproduction, at all events, yielded zygospores in moderate quantity. The development of these bodies occurred only where two main mycelial filaments crossed or came close together (FIG. 2, *A–C: a, b*). Paired zygophoric branches invariably arose from separate filaments; their growth taking place with abrupt changes in direction (FIG. 2, *A*), together sometimes with meager branching and haphazard intrication (FIG. 2, *B, c, d*). Now and then the paired branches became more pronouncedly intricated by winding helically about each other (FIG. 2, *C*). After the sexual branches had united apically, the globose zygosporangium sometimes grew out from near the union (FIG. 2, *B, c*), but no less often it was formed on a stalk, about 5 μ long, arising from near the union (FIG. 2, *A; B, d*); and in other instances it developed laterally on one of the zygophoric branches, as much as 15 μ below the fused tip (FIG. 2, *C*). When the zygosporangium had attained a diameter of 14 to 16 μ, its growth ceased, and its spherical membrane became thickened unevenly in being transformed into a somewhat crustose, externally corru-

gated yellow envelope (FIG. 2, *D*). Directly under this envelope the zygospore wall was then laid down as a colorless layer with a uniform thickness of about 1 μ. The contents of the more mature zygospores consisted in large part of coarsely and uniformly granular material, within which were discernible from 5 to 10 homogeneous reserve globules, mostly 2.5 to 3.5 μ in diameter, together with at least one refringent body (FIG. 2, *D*).

THE SEXUAL STAGE OF COCHLONEMA PUMILUM

In a maizemeal-agar plate culture that after being permeated with *Pythium* mycelium had been further planted with a small quantity of leaf mold taken from deciduous woods near Fairfax, Va., on November 10, 1942, there was observed 28 days later some development of the small endoparasite I described in a previous paper (**17**) as *Cochlonema pumilum.* The fungus subsisted evidently on the same protozoan species that it had attacked in the earlier material; the identity of the testaceous host animal being especially clear since more than a few of the parasitized individuals measured only 20 to 25 μ in length (FIG. 3, *A*, *B*), and thus shared the small dimensions noted in my earlier account. However, most of the individual rhizopods were of greater size, measuring commonly from 30 to 38 μ in length and from 18 to 22 μ in width (FIG. 3, *C–M*), and therefore offered better agreement with Wailes' (**35**) description of *Euglypha laevis* (Ehrenb.) Perty, the species to which the host animal was referred. Despite the frequent presence of plural conidia within them (FIG. 3, *C*), the larger infected animals, like the smaller ones, were never seen to contain more than a single thallus; so that the thalli here attained greater dimensions and naturally, when asexual reproduction supervened, gave rise to correspondingly more abundant conidial apparatus. Thus, in many instances, 3 or 4 conidial chains, each about 500 μ long, were found arising from near the mouth of the empty host testa; the total number of conidia then produced being about 3 or 4 times greater than had been observed in the earlier material where only small animals were present.

Although the larger number of thalli in the culture expended their protoplasmic materials entirely in giving rise to conidial

apparatus, sexual reproduction by development of zygospores was, nevertheless, rather frequent, being displayed by relatively small thalli within small animals (FIG. 3, *B*) as well as by the more robust thalli within the larger animals (FIG. 3, *D–M*). If occasionally—perhaps in one among fifteen or twenty instances—a thallus showed evidence of having given rise to some conidia before initiating development of a zygospore, it was yet much more usual for the individual thallus either to form conidial apparatus exclusively, or to devote all its contents to the production of a single zygospore. The earlier stages of sexual reproduction never came under observation, nor did the sexual apparatus whose development had begun show any further development in any of the several 8-hour periods during which it was studied under the microscope. This persistent inactivity has meaning in itself, since, in general, sexual development among the Zoopagaceae is not, as with species of *Pythium* and *Phytophthora*, for example, adversely affected by the environal conditions attending microscopic inspection, but on the contrary, is often encouraged by them. From analogy with the congeneric form I described as *Cochlonema symplocum* (19) there is reason to presume that sexual development was at a standstill during the periods of observation because of unsuitably high temperatures—75° to 85°C.—maintained in the laboratory during working days in winter, and that it was initiated and could proceed only at the lower temperatures intervening on week-ends and during periods of unusually cold weather.

Whatever may be the environal conditions governing its development, the globose zygosporangium of *Cochlonema pumilum* is always formed in a position approximately between the two ends of the thallus. As the thallus is strongly curved, its ends are usually close together when definitive size is attained; so that from spatial necessities, the globose cell often comes to extend backward toward the fundus of the animal host (FIG. 3, *D*, *F*, *L*), or to lie for the most part to one side of the plane of the thallus (FIG. 3, *E*, *J*), or to jut forward toward the mouth of the animal host (FIG. 3, *B*). In favorable instances where a profile view is afforded of relationship between thallus and zygosporangium, a structural connection is sometimes discernible between the

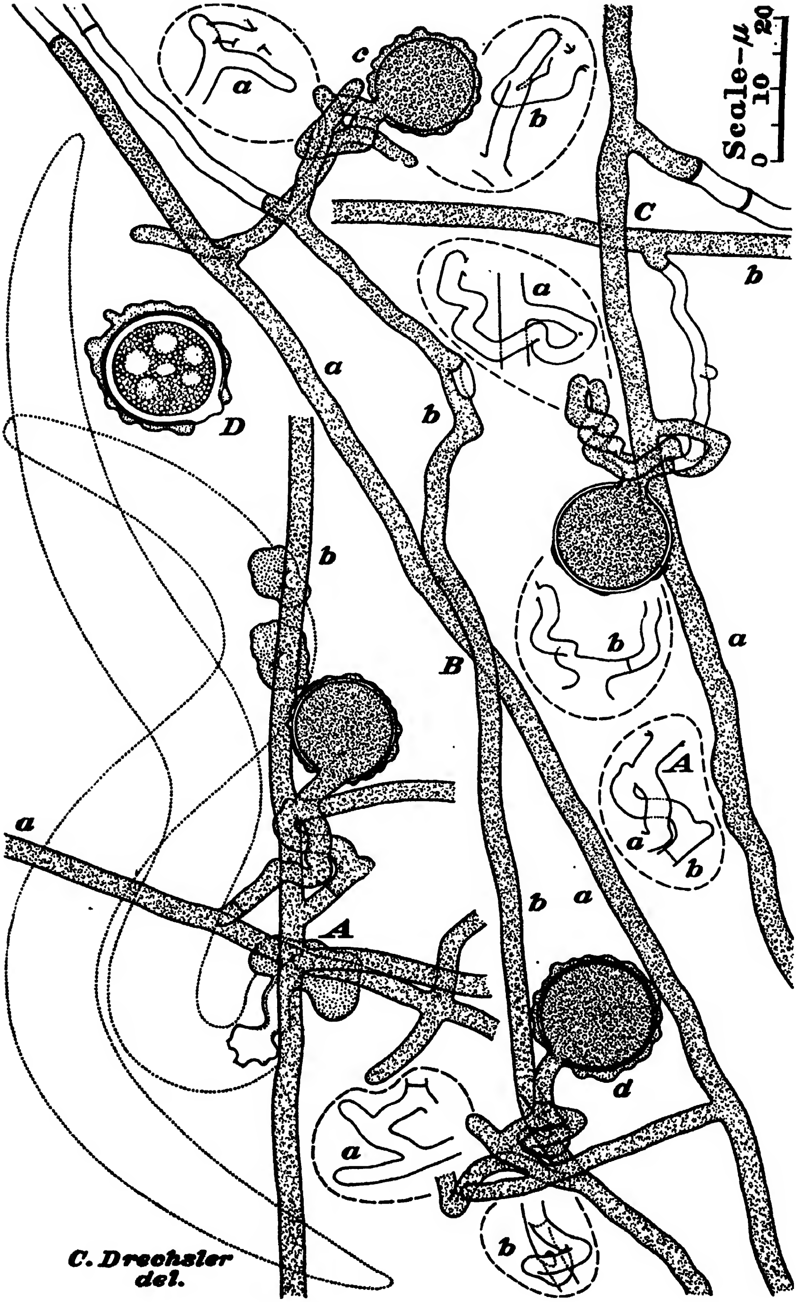

FIG. 2. Sexual stage of a nematode-capturing fungus belonging in the Zoopagaceae.

proximal end of the thallus and the zygosporangium (FIG. 3, *D*, *K*), while at other times the distal end of the thallus appears united to the zygosporangium (FIG. 3, *B*, *F*), and somewhat rarely both ends of the thallus seem joined to the zygosporangium (FIG. 3, *G*). Although now and then (FIG. 3, *K*) the zygosporangium shows such broad attachment to the thallus that hardly any modification in the thallodic extremity would need to be assumed, more often a narrowing of the thallodic extremity suggests that a short prolongation, interpretable as a zygophoric branch, must have been put forth to initiate sexual development (FIG. 3, *D*, *E*, *F*).

In the production of a zygospore, just as in the production of conidia, the distal portion of the thallus is always evacuated first; its membrane often being found empty and somewhat collapsed at a stage when the proximal portion is still, through increasing vacuolization, contributing its protoplasm to the growing zygosporangium (FIG. 3, *E*, *F*, *G*, *K*). Even after it has lost all its contents, the proximal part retains its original outline rather well, giving the impression that it is surrounded by a sturdier wall (FIG. 3, *D*, *H*, *I*, *J*) than the distal part. Where, as is often true, the empty thallodic envelope contains only the one partition that separates the collapsed distal part from the unshrunken proximal part (FIG. 3, *B*, *J*, *L*, *M*), the whole apparatus usually offers an appearance strongly suggestive of a developmental sequence as follows: (1) division of the thallus into two gametangia; (2) conjugation between two short zygophoric prolongations put forth, respectively, from the proximal end of the proximal gametangium and the distal end of the distal gametangium; and (3) production of a zygospore at or near the place of conjugation. As nothing has been observed directly at variance with such a developmental sequence, it is held to prevail generally in the species; though, owing mainly to optical difficulties usual in parasitized testaceous rhizopods, many specimens are so ambiguous in what they reveal that if they were considered individually other interpretations might be entertained.

Thus, in the numerous examples where the relationship of the zygosporangium to the thallus is not shown in profile, and more especially in the many examples where one or both ends of the

thallus lie concealed under the zygosporangium, double attachment of the globose body is neither visible nor directly surmisable; so that development of an azygospore rather than of a zygospore might be in progress. However, if azygospore formation were at all frequent, occasional specimens should reveal one end of the thallus to be free and clearly separated from the globose body—a condition that has not been observed so far. Then, too, where double attachment of the globose body to the thallus cannot be made out, a possibility exists that a supernumerary conidium, perhaps concealed under the globose body itself, may have taken part in the antecedent sexual union after the manner of conidia in the allied forms I have described as *Stylopage cephalote* (**15**) and *Acaulopage marantica* (**16**). If such conidium-thallus conjugation prevailed clear instances of it should now and then be discernible; but no clear instances have come to light, and although in one case the zygosporangium appeared intercalated between the thallus and an empty conidial envelope (FIG. 3, *K*), the relationship of parts found here was best explained on the assumption that the empty conidium was the spore-parent of the thallus, and that it came into its unusually distant position through the development of the zygosporangium at the juncture of its germ tube with the thallus. Again, some little ambiguity not, however, attributable to optical difficulties arises frequently in specimens where the thallus, after yielding its contents to the zygosporangium, shows two (FIG. 3, *I*) or even three (FIG. 3, *D, II*) transverse partitions; the plural cross-walls, of course, making for an appearance less suggestive of division into two gametangia that is offered by specimens with only one cross-wall. Since the extra partitions are manifestly laid down as retaining walls in the progressive evacuation more particularly of the longer proximal thallodic segment that presumably constitutes the proximal gametangium, they can hardly be considered to have much special significance.

Once the thallus has been completely evacuated, a thick, distinctly yellowish zygospore wall with a scalloped outer contour is laid down close under the colorless and slightly collapsed zygosporangial envelope (FIG. 3, *H, I, J*). This wall surrounds rather coarsely granular protoplasm within which, at full maturity, one

or two reserve globules and one or two smaller refringent bodies are often somewhat indistinctly discernible (FIG. 3, *B*, *L*, *M*). As only a single thallus develops within the individual animal host, and as in instances of sexual development the entire protoplasmic contents of the thallus are usually given to the single zygosporangium, it is not surprising that the dimensions of the zygosporangium and zygospore, like those of the thallus, are governed mainly by the dimensions of the infected protozoan. For a fungus which in its vegetative body, as also in its asexual reproductive structures, is rather small in comparison with allied forms, the sexual structure may be considered somewhat large—the diameter of the zygosporangium varying mostly from 9 to 15 μ, and that of the zygospore from 8 to 14 μ. The zygospore wall was found ranging from .8 to 2.2 μ in thickness, while the protoplast surrounded by it varied from 5.5 to 10 μ in diameter.

A BRANCHED COCHLONEMA PARASITIC ON A TESTACEOUS PROTOZOAN

A maizemeal-agar plate culture that after being permeated with *Pythium* mycelium had been further planted on Jan. 20, 1937, with leaf mold newly collected from deciduous woods in Arlington, Va., revealed when examined 3 months later about 50 specimens of a testaceous rhizopod from each of which ascended a few chains of cylindrical conidia generally similar to the conidial chains of *Cochlonema pumilum* and of the congeneric form I described earlier as *C. cylindricum* (**14**). Although no living specimen of the animal could be found, the well preserved testae (FIG. 3, *N*, *O*) were without much difficulty referred to *Sphenoderia dentata* Penard (**28**)—the same species, therefore, that later (**17**) was observed parasitized by my *C. fusisporum* and my *Pedilospora dactylopaga*. Within each testa was seen an empty convolved thallus differing from the thalli of *C. pumilum* and *C. cylindricum* in being consistently branched. The branching, if mainly of the dichotomous type, was much less regularly dichotomous than is usual in the genera *Cochlonema* and *Endocochlus*. In most instances a strongly curved hyphal trunk was usually recognizable, which from a position often somewhat closer to its base than to its tip gave off monopodially

a short stout branch that at once broadened into 2 lobes (FIG. 3, *N*) or divided dichotomously into 2 short arms. In addition, the hyphal trunk frequently bore a short stout branch near its distal end (FIG. 3, *N*).

The empty thalli contained usually from 2 to 4 cross-walls, which manifestly had been laid down as retaining walls during the progressive evacuation of protoplasm by way of the single reproductive filament. This filament, as in all related species, followed a somewhat irregular course through the mouth of the animal, to give rise externally to the several conidial chains whereby the presence of the parasite had been betrayed. When mounted for examination under a cover glass, the chains crumbled into their component spores. These spores (FIG. 3, *P*) were found to be slightly wider than those of *Cochlonema cylindricum*, and in more noticeable measure wider than the similarly cylindrical spores of *C. pumilum*.

As the fungus seems rather markedly distinguished from its two most closely related congeners by the character of its thallus, it is described under a specific name meaning "branched."

Cochlonema ozotum sp. nov.

Hyphae alitae incoloratae, saepius 40–45 μ longae, 6–7 μ crassae, axe plerumque semel convolutae, vulgo in medio et prope apicem ramis simplicibus vel bifidatis vel bifurcis praeditae, ex basi per os animalis hypham genitabilem circa 1.5 μ crassam proferentes quae 2–3 catenulas conidiorum 300–750 μ longas profert; conidiis incoloratis, cylindraceis, utrimque leviter rotundatis, vulgo 4.6–8 μ longis, 1.3–1.5 μ crassis.

Sphenoderiam dentatam interficiens habitat in humo silvestri in Arlington, Virginia.

Vegetative hyphae colorless, often 40 to 45 μ long, 6 to 7 μ wide, with respect to their main axis circularly convolved in one turn, provided with branches near the apex and also in a position nearly midway between base and apex, the branches whether simple or bifid or forked being short and stout; each vegetative hypha extending from its base and through the mouth of the animal host a colorless reproductive hypha, about 1.5 μ wide, which sends up usually 2 or 3 colorless hyphae 300 to 750 μ long to be transformed into chains of closely arranged conidia; these conidia of cylindrical shape, with slightly convexed ends, colorless, measuring mostly 4.6 to 8 μ in length and 1.3 to 1.5 μ in width.

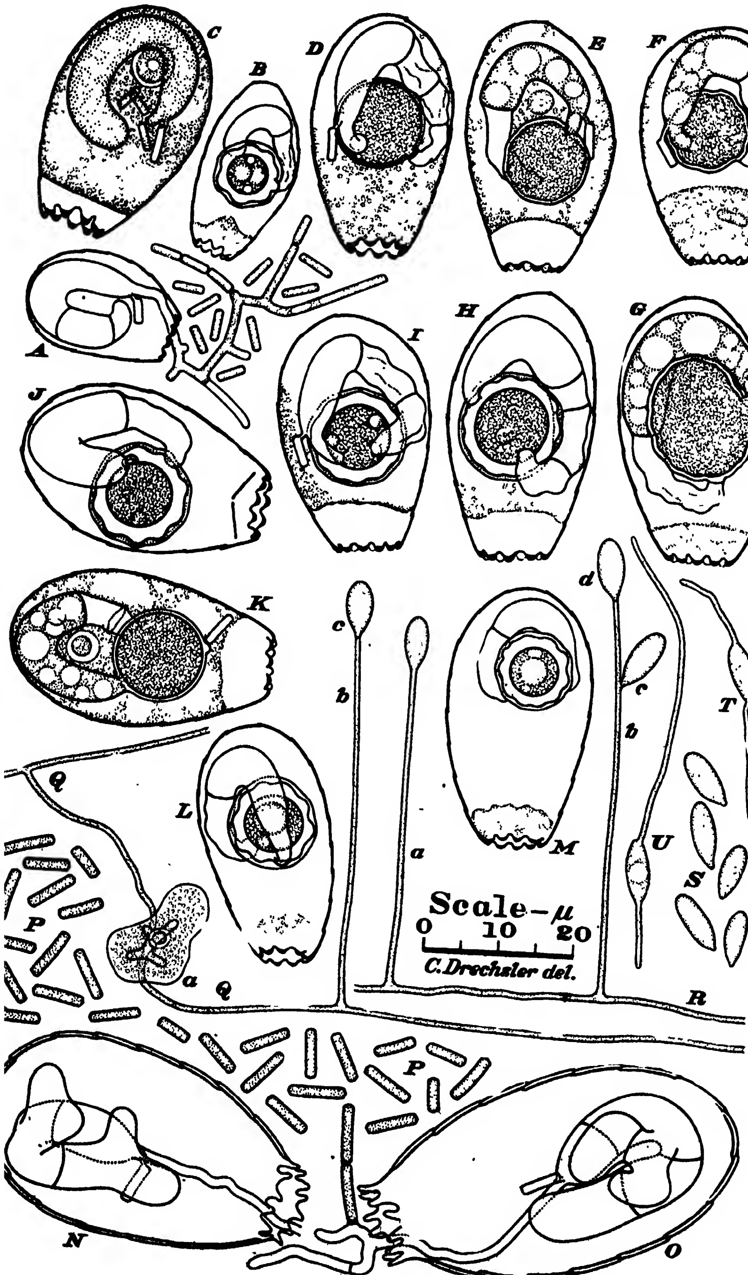

FIG. 3. *A–M, Cochlonema pumilum; N–P, Cochlonema ozotum; Q–U, Stylopage minutula.*

Destructive to *Sphenoderia dentata* it occurs in leaf mold in Arlington, Va.

A MINUTE SPECIES OF STYLOPAGE WITH PLUMP CONIDIA

A maizemeal-agar plate culture that after being permeated with *Pythium* mycelium had been further planted on Dec. 14, 1936, with leaf mold newly collected from deciduous woods in Arlington, Va., revealed on examination 17 days later some development of a sparse mycelium composed of very delicate hyphae (FIG. 3, *Q*, *R*) along which minute *Amoebae* (FIG. 3, *Q*, *a*) were held attached by means of yellow adhesive material. The captured animals, mostly 7 to 15 μ wide when drawn into a rounded form, contained in their colorless protoplasm a single subspherical nucleus, about 2.5 μ in diameter, wherein was visible a slightly darker globose part approximately 1.8 μ in diameter. A dichotomous haustorium with noticeably swollen, digitate assimilative branches was extended into each captive. After it had taken up the cell contents of the prey, the haustorium in turn became evacuated, through withdrawal of its protoplasm backward into the parent hypha; whereupon its empty membrane, as also the collapsed protozoan integument, soon disappeared from view.

The fungus displayed meager asexual reproduction in sending up sparsely scattered delicate conidiophores from hyphae prostrate on the substratum. These conidiophores (FIG. 3, *Q*, *b*; *R*, *a*) were often found bearing only a single conidium of elongate obovate shape (FIG. 3, *Q*, *c*), but frequently, too, after having produced one conidium they resumed growth to produce another on the new apex (FIG. 3, *R*, *b*, *c*, *d*). When conidia became detached (FIG. 3, *S*) and fell on the moist agar substratum, they germinated readily; in most instances they extended a delicate germ tube from each end (FIG. 3, *T*, *U*).

With respect to its generally minute dimensions the fungus shows close resemblance to the delicate congeneric species I described earlier as *Stylopage lepte* (10). Its conidia, however, are conspicuously shorter and broader than those of *S. lepte;* their shape being suggestive rather of *S. hadra* and *S. leiohypha*. In

comparison, more especially, with these two robust forms the fungus appears well deserving of the name here applied to it.

Stylopage minutula sp. nov.

Mycelium sparsum; hyphis sterilibus continuis, incoloratis, parce ramosis, vulgo .6–.9 μ crassis, ad animalia minuta inhaerentibus, pelliculam cujusque capti perforantibus, haustorium intus evolventibus quod carmen exhaurit; haustorio basi semel vel bis dichotomo, ita 2–4 ramulos 1–1.3 μ crassos ferente; hyphis fertilibus continuis, erectis, incoloratis, saepe 40–60 μ altis, .6–.9 μ crassis, uno conidio genito saepe repullulantibus et aliud conidium gerentibus; conidiis incoloratis, ellipsoideis vel elongato-obovoideis, basi paulo acutis, 7.5–9 μ longis, 2.6–3.6 μ crassos.

Amoebas plerumque 7–15 μ latas capiens consumensque habitat in humo silvestri in Arlington, Virginia.

Mycelium sparse; vegetative hyphae continuous, colorless, filiform, sparingly branched, commonly .6 to .9 μ wide, adhering to minute animals, perforating the pellicle of each captive and intruding a haustorium which bifurcates once or twice near its base to terminate in 2 to 4 short digitate assimilative branches 1 to 1.3 μ wide. Conidiophores continuous, colorless, erect, often 40 to 60 μ long and .6 to .9 μ wide, after producing a first conidium terminally often elongating to bear a second one; conidia unseptate, colorless, ellipsoidal or elongate obovoid, often slightly pointed at the base, commonly measuring 7.5 to 9 μ in length and 2.6 to 3.6 μ in width.

Capturing and consuming *Amoebae* mostly 7 to 15 μ wide it occurs in leaf mold in Arlington, Va.

A SPECIES OF ACAULOPAGE WITH APPENDAGED DICHOTOMOUS CONIDIA

Several maizemeal-agar plate cultures that were started with decaying pieces of waterlily (*Nymphaea odorata* Ait. and *N. tuberosa* Paine) leaves collected near Butternut, Wis., on July 12, 1935, permitted abundant development of a zoopagaceous fungus resembling in varying degree the congeneric forms I have described under the binomials *Acaulopage macrospora*, *A. ceratospora*, and *A. tetraceros* (**10**). On its sparingly branched mycelium (FIG. 4, *A–E*) *Amoebae* from 5 to 20 μ in diameter were found attached by means of yellow adhesive material. The smallest of the captured animals were seen invaded usually by a single assimilative branch, slightly narrower than the parent filament (FIG. 4, *A*, *a*, *c*; *B*). In animals of somewhat greater

dimensions the infective process, after penetrating the integument, would often divide into 2 assimilative branches (FIG. 4, *A*, *b*, *d*, *e*, *f*; *C*; *D*), while in the largest prey that came under observation the sarcode was permeated by a bush-like haustorium with as many as 5 branches (FIG. 4, *E*).

Thus nourished on *Amoebae*, apparently to the exclusion of other sources of food, the fungus gave rise to conidia on hyphae (FIG. 4, *F*, *G*) that seemed to be narrower and to ramify somewhat more freely than the predaceous filaments. As these hyphae often revealed distally a rather abrupt curvature, not unlike the curvature familiar in fertile hyphae of *Acaulopage tetraceros*, there was reason to suspect that the conidia formed terminally on them should normally have stood erect. However, in the presence of nematodes and mites, even the conidia whose unbranched clavate form betokened an early stage of development (FIG. 4, *F*, *G*) were mostly found prostrate on the substratum. During their later stages of growth the conidia would bifurcate distally at an angle usually approximating a right angle (FIG. 4, *H–N*); the primary bifurcation often being followed by a secondary bifurcation in one of the two divergent arms (FIG. 4, *O–R*), and occasionally by bifurcation in both arms (FIG. 4, *S*). When branching was concluded the terminal prongs, whether 2, 3, or 4 in number, were partly emptied by retraction of protoplasm, the emptied part of each prong persisting as a membranous appendage. Now and then a terminal prong, especially if undersized, retained its contents throughout (FIG. 4, *M*), but on the other hand some conidia became emptied not only distally in their prongs, but also in lesser measure, proximally through withdrawal of contents from a small conical part at the base (FIG. 4, *H*, *I*, *J*, *L*).

An epithet having reference to the characteristic branching of its conidia may serve in distinguishing the fungus from the several appendaged species most closely related to it.

Acaulopage dichotoma sp. nov.

Mycelium sparsum, hyphis sterilibus continuis, incoloratis, parce ramosis, 1.3–1.6 μ crassis, ad animalia minuta inhaerentibus, pelliculam cujusque capti perforantibus, haustorium intus evolventibus quod protoplasma exhaurit; haustorio nunc simplici nunc ad instar arbusculae ex 2–5 ramulis assumentibus

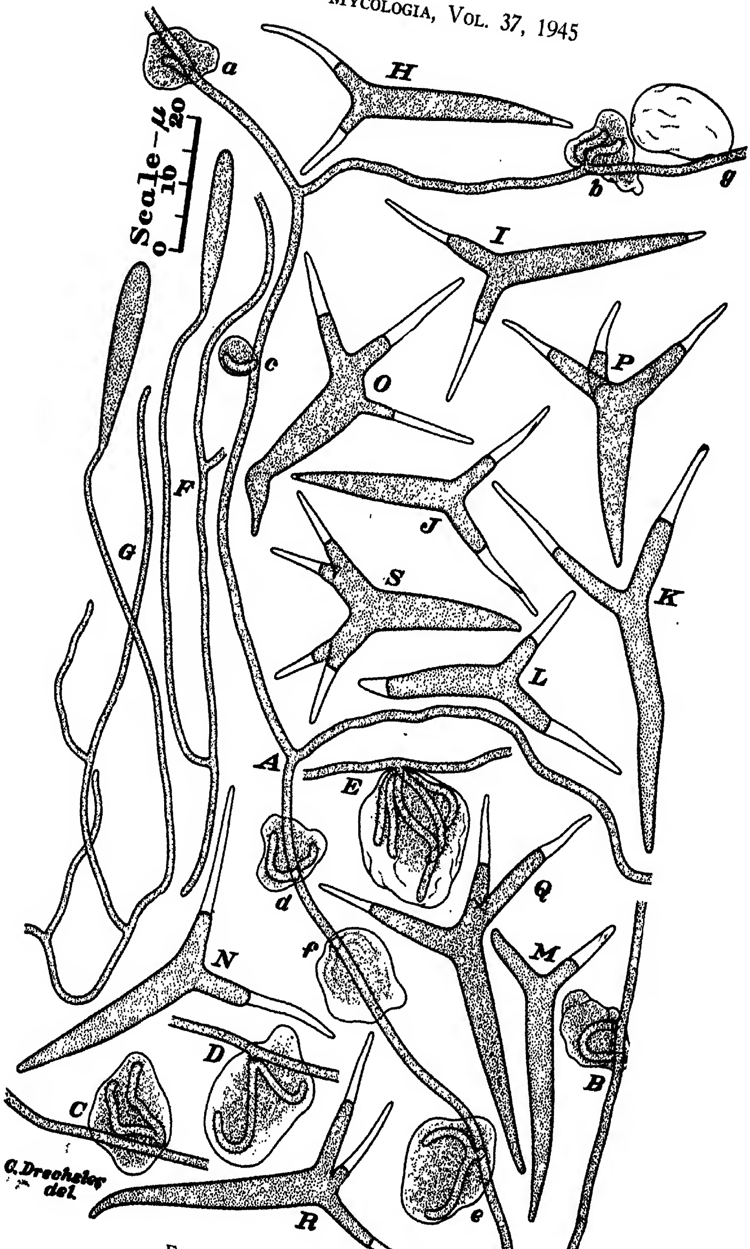

FIG. 4. *Acaulopage dichotoma.*

5–25 μ longis 1.2 μ crassis constante. Hyphae fertiles continuae, incoloratae, mediocriter ramosae, vulgo circa 1 μ crassae, apice conidia singulatim gignentes; conidiis incoloratis, plerumque semel vel bis bifurcis, itaque vulgo ypsiliformibus vel tricornibus vel quadridentibus, trunco eorum inversum conico, saepe 25–40 μ longo, sursum 4.5–7 μ crasso quandoque in parte infima 1–5 μ longa vacuo, ramis eorum cornuatis divaricatis, 10–30 μ longis, deorsum 2–5 μ crassis primum protoplasmatis omnino repletis mox in parte supera 5–20 μ longa fere inanibus.

Amoebas 5–20 μ latas capiens consumensque habitat in foliis putrescentibus Nymphaeae odoratae et Nymphaeae tuberosae prope Butternut, Wisconsin.

Mycelium sparse; vegetative hyphae continuous, colorless, sparingly branched, 1.3 to 1.6 μ wide, capturing small animals by means of yellow adhesive material, perforating the pellicle of each captive and intruding a haustorium which may consist of a simple branch or of 2 to 5 branches, 5 to 25 μ long, about 1.2 μ wide, in bush-like arrangement. Conidiophorous hyphae continuous, colorless, moderately branched, usually about 1 μ wide, producing conidia singly at the tip. Conidia colorless, mostly branched dichotomously once or twice to terminate in 2, 3, or 4 tapering divergent prongs; the main axial part of the spore obconical, often 25 to 40 μ long, 4.5 to 7 μ wide distally, sometimes empty at the base for a distance of 1 to 5 μ; the prongs mostly 10 to 30 μ long, 2 to 5 μ wide proximally, at first filled with protoplasm throughout but nearly always soon becoming empty distally for a distance of 5 to 20 μ.

Capturing and consuming *Amoebae* 5 to 20 μ wide it occurs in decaying leaves of *Nymphaea odorata* and *Nymphaea tuberosa* near Butternut, Wis.

TAXONOMIC CONSIDERATIONS RELATING MORE ESPECIALLY TO CYSTOPAGE INTERCALARIS AND ZOOPHAGUS INSIDIANS SOMMERSTORFF

Although at first sight such types of conidial apparatus as are produced by *Cochlonema ozotum* and *Stylopage minutula* look commonplace and generally insignificant, they nevertheless prove to an unusual degree adequate for taxonomic purposes once they are known to be associated with a thallus or mycelium in which cross-walls are never laid down as partitions between adjacent living vegetative cells. Unfortunately the intercalary and frequently intramatrical chlamydospores of *Cystopage intercalaris* have far less distinctiveness, since resting bodies not greatly different from them are formed in various species of Oomycetes

and Zygomycetes. In particular, as has been noted, the chlamydospores of *C. intercalaris* strikingly resemble the conidia of some widely familiar species of *Pythium*. When they are compared, for example, with the conidia of *P. ultimum* Trow, a species often occurring as causal agent of root rot in the same vegetable materials as *C. intercalaris*, a close similarity is revealed with respect to shape, to size, to manner of attachment, to texture of the densely granular porridge-like protoplasmic contents, and to mode of germination by production of vegetative hyphae. While such correspondence in structural features might, by itself, have only rather slight descriptive interest, it becomes deserving of more attention from the fact that the rotifer-capturing *Zoophagus insidians* Somm., concerning which an unusually copious literature is available, has for the most part been treated, because of reported similarity in zoospore development, as being either closely related to *Pythium* (**31**) or as belonging in *Pythium* (**23**). Under the circumstances a suspicion could naturally arise that the chlamydospores of *C. intercalaris*, like the conidia of *P. ultimum*, might well be homologous with the globose zoosporangia of such species of *Pythium* as *P. Debaryanum* Hesse, and that, consequently, the fungus producing them might perhaps belong in the Pythiaceae rather than in the Zoopagaceae. The features suggestive of relationship in the Pythiaceae need to be examined in conjunction with developmental features ascribed to *S. insidians* that would seem to reveal more credible homologies with typical conidium-producing members of the Zoopagaceae.

Sommerstorff's (**29**) only observations possibly relating to reproduction of the predaceous fungus described by him were made on a single specimen of rotifer whose unattached dead body he found occupied by evacuated hyphae from which extended eruptive branches, open at the tip. Lying near this dead animal were seen numerous empty globose cysts, about 10 μ in diameter, and also a clustered aggregation of approximately 8 zoospore-like amoeboid cells. After some rotational and trembling movements these cells came to rest, rounded up, and encysted. On the following morning only empty envelopes remained where the cysts had been, the protoplasts evidently having escaped following extension of a short germ tube. Sommerstorff regarded this

isolated instance of zoospore formation insufficient for any statement regarding the systematic position of his fungus, and merely ventured the opinion that since he was dealing with a phycomycete of aquatic habit propagation by zoospores, as in the Saprolegniales, was not improbable. The sequence of conditions described by him would, indeed, seem to correspond better to zoospore development in the Saprolegniaceae than to zoospore development in the Pythiaceae. At all events the free unattached condition of the dead rotifer appears less indicative of destruction by a fungus given habitually to a predaceous mode of attack than to destruction by a fungus which either is addicted exclusively, like *Hydatinophagus Apsteinii* Valk. (**32**, **33**), to attacking rotifers in some usual parasitic manner, or, like *Sommerstorffia spinosa* Arn. (**2**), displays both ordinary parasitic attack by means of zoospores and predaceous attack through capture by means of adhesive organs. The meager persuasiveness of Sommerstorff's taxonomic comment was abated further by Mirande's (**27**) report that though several times he found similar cysts on rotifers attacked by *Zoophagus insidians*, closer examination always showed them to represent a superadded chytrid.

In Gicklhorn's (**24**) account *Zoophagus insidians* is set forth as giving rise within the host animal to large sporangia, spherical in shape or often protruding distally, each delimited at the base by a thick septum; the sporangial contents, consisting of numerous immotile individualized zoospores imbedded in slime, reaching the exterior after rupture of the distal protrusion; the slime thereupon swelling rapidly, and the zoospores escaping as laterally biciliate motile swarmers. From the magnification indicated for the figures illustrating them, the zoospores would appear to measure only about 2.5 μ in diameter. The small size of these bodies, their very distinct individualization within the sporangium, and their emission in a matrix of slime, are features unparalleled in *Pythium;* yet Gicklhorn assigned the fungus to a position within the Pythiaceae close to that genus. He described a further type of asexual reproduction, wherein hyphae, 5 to 10 μ wide, after growing out of the animal abstrict terminally a number of globose conidia, about 15 μ in diameter, which collect in a

botryose or capitate cluster, eventually to fall off and to germinate by producing individually a predaceous hypha.

The sporulation that Gicklhorn took for conidial development was interpreted by Arnaudow (3) as more probably representing zoospore production of the same type he himself found in *Zoophagus insidians* (1). In this type of zoospore production, we are told, development follows the course characteristic of *Pythium*, but after the laterally biciliate zoospores, about 10 μ wide, have come to rest and rounded up they escape from the cyst envelope and again swim about as laterally biciliate swarmers, to encyst, eventually, a second time. This iterant swarming Arnaudow regarded as diplanetism of a sort not known, as far as he could ascertain, among other fungi; wherefore he concluded that the zoosporangia in question could not belong to some other aquatic fungus, were the possibility to be considered that alien phycomycetes might occur within captured animals in the role of table companions. Now, the repetitional development which Arnaudow held to be unknown elsewhere had in fact been adequately set forth 14 years earlier in Butler's (4) original description of *P. diacarpum*. Later, quite similar development was reported as occurring also in *P. Butleri* Subr. (5), in *P. dissotocum* Drechsl. (6, 18), in *P. adhaerens* Sparrow (30), in *P. angustatum* Sparrow (30), and in *P. epigynum* Höhnk (25). The zoosporangial stage observed by Arnaudow would seem, therefore, all the more certainly referable to the Pythiaceae; but, on the other hand, this stage can no longer be held necessarily connected with *Z. insidians* on the ground that it is absent elsewhere. Increased significance might consequently be read into Arnaudow's admission that with the cultural methods he employed his demonstration of connection between the observed zoosporangia and *Z. insidians* was not to be regarded as complete (nicht als lückenlos). The uncertainty expressed in this admission was, however, strongly disclaimed by Valkanow (34) who on encountering *Z. insidians* three times in his freshwater aquaria made observations which, we are told, not only confirmed Arnaudow's description of sporangial structure but also uncovered in stained preparations a very clearly visible connection between the mycelium and the evacuation tube of the sporangium. From a conviction, apparently,

that the number of swimming stages passed through by zoospores after their individualization is here of more moment taxonomically than the condition in which the sporangial contents are discharged, Valkanow referred the fungus to a position in the Saprolegniaceae near the three *Aphanomyces*-like genera *Synchaetophagus*, *Hydatinophagus*, and *Sommerstorffia*.

Whatever doubts Arnaudow may have had concerning the realty of zoospore development in ***Zoophagus insidians*** assuredly did not apply to a second type of asexual reproduction described by him, wherein a mycelial filament, through terminal budding, would give rise, following repeated subapical elongation, to a succession of eelworm-shaped bodies, 260 to 300 μ long and up to 14 μ wide. These bodies he designated as gemmae, though explaining that unlike the gemmae in species of *Saprolegnia* they did not represent functionally frustrated oogonia, or frustrated sporangia, or mycelial segments delimited by cross-walls. His description of their development offers obvious correspondence more especially to conidial development in the zoopagaceous form I have described as *Stylopage rhabdospora* (**13**), though their reported disarticulation previous to any septation or evacuation of the slender frangible sterigmatic attachment would seem alien to all modes of conidial disjunction so far observed in known members of the Zoopagaceae. In *Z. tentaclum*, judging from Karling's (**26**) original description of this somewhat smaller congeneric rotifer-capturing species, elongated fusiform gemmae or conidia, unquestionably homologous to those of *Z. insidians*, are not only produced but also become disjointed after a manner familiar among the Zoopagaceae: the production of these spindle-shaped bodies, like the production, again, of conidia in *S. rhabdospora*, taking place successively at the tips of fertile hyphae given to repeated subapical prolongation; their disjunction thereupon being accomplished, much like conidial disarticulation in my *Cochlonema nematospora* (**13**) and my *C. megaspirema* (**14**), after evacuation of protoplasm from the narrow sterigmatic attachment has been followed by deposition of retaining walls at the ends of the separated protoplasts. The presence of a number of septa within the several gemmae of *Z. insidians* that were figured by Arnaudow in advanced stages of germination, makes for

further correspondence with the conidia of *S. rhabdospora*, since the latter, too, lay down retaining walls as their contents migrate progressively into elongating germ hyphae. Though containing a manifestly large mass of protoplasm newly elaborated during periods when abundant nourishment sustained high vegetative vigor, the gemmae of *Z. insidians* always gave rise to predaceous mycelia, never being found undergoing conversion into zoosporangia. This was true also of the conidia of *Z. tentaclum* whose content of protoplasm should be sufficient for fairly liberal zoospore production even if their more modest measurements—40 to 80 μ in length and 3 to 6.5 μ in width—brings them well within the range of dimensions displayed by the conidia of known members of the Zoopagaceae. Indeed, zoosporangia were not seen in *Z. tentaclum* at all, nor, for that matter, antheridia and oogonia.

The sexual stage found by Arnaudow in *Zoophagus insidians*—its connection with the rotifer-capturing vegetative stage would seem amply attested by the predaceous spurs shown arising from the undulating sexual branches as well as from the main hyphae bearing these branches (**3**: *fig. 5*)—was considered by him to indicate relationship of the fungus in the Pythiaceae rather than in the Saprolegniaceae. However, his illustrations of the sexual stage seem rather more strongly suggestive of the Zoopagaceae than of any other family of Phycomycetes. Certainly in the Zoopagaceae it is more usual than in the Pythiaceae for the sexual branches to make contact with each other before they have become differentiated distally into conjugating organs; and much more usual, also, for these branches to fuse apically and to lay down a special cross-wall soon after they have been brought together—at a time, that is, when the materials required for the formation of a zygospore have only in small part been accumulated locally. While in some species of *Pythium*, as notably in *P. vexans* deBary, the sexual branches likewise are brought together very early, so that the oogonium and the antheridium develop in intimate contact with each other, these organs are not ordinarily delimited by cross-walls until on reaching their definitive size they contain all the protoplasmic materials destined to enter into the formation of the oospore. Again, while

in many species of *Pythium*, as, for example, in *P. ultimum*, an intercalary antheridium consisting of a segment of the oogonial hypha adjacent to the oogonium may not be distinguished outwardly from other filamentous parts, an antheridium borne terminally on a branch is nearly always distinguishable from neighboring hyphal parts by its greater width or, perhaps, by its clavate or crook-necked shape. Now, as the sexual apparatus ascribed to *Z. insidians* is of strictly diclinous origin, all antheridia present should be of the more easily recognizable type. Yet none of the hyphal parts attached to the 3 globose bodies drawn by Arnaudow as representing nearly mature oogonia (**3**: *fig. 5, L, M, N*) show any modification marking them as antheridia of a pythiaceous fungus. For this reason, mostly, the 3 units of sexual apparatus show less resemblance to diclinous sexual apparatus of any species of *Pythium* with which I am acquainted than to the diclinous sexual apparatus of those species in the Zoopagaceae—*Zoopage phanera* Drechsl. (**9**) and *Z. atractospora* Drechsl. (**13**) may be cited as examples—wherein the zygophoric branches become neither much swollen nor spirally intervolved, and wherein the zygosporangium develops in an intercalary position not far from the juncture of the gametangial elements.

From resemblances both in its sexual and its asexual development Arnaudow's gemma-producing fungus would seem to belong more probably in the Zoopagaceae than in the Pythiaceae or Saprolegniaceae. Among known members of the Zoopagaceae its production of gemmae successively on repeatedly elongated submerged hyphae finds ecological parallelism in the normally submerged conidial development of my *Stylopage scoliospora* (**17**); the asexual reproductive bodies of the two species alike expressing in their unbranched unappendaged condition adaptation to a submerged mode of life, and alike offering contrast with the conidia of *Acaulopage dichotoma*, which through their branched and appendaged condition more nearly betray adaptation to a floating aquatic existence. It must be admitted, of course, that all correspondence between the gemma-producing fungus and the Zoopagaceae would need to be regarded as illustrative of convergence, and as being wholly without taxonomic import, should

the production of gemmae described by Arnaudow prove to be unmistakably associated with zoosporangial development in one and the same fungus. The evidence hitherto given in favor of such association appears far from decisive; for Arnaudow, as has been noted, explicitly admitted some uncertainly in regard to the connection between his *Pythium*-like zoosporangia and his *Zoophagus insidians*, while Valkanow in claiming to have observed an unambiguous connection between evacuation tube and mycelium did not state that the mycelium in question also gave rise to gemmae. There is reason to suspect, certainly, that the binomial which Sommerstorff established on a purely vegetative stage has been applied by different investigators to fungi widely different in manner of reproduction and in taxonomic relationships. No diversity of application, however, can account for the curious fact that of the several investigators who from first-hand observations ventured to assign the species to the Oomycetes, the one who assigned it most unreservedly to the Pythiaceae ascribed to it a type of reproduction wholly alien to that family, whereas the one who claimed to have found its rotifer-capturing mycelium most unmistakably connected with apparatus serving in zoospore development of a type frequent in *Pythium* insisted emphatically that the species cannot correctly be referred to the Pythiaceae.

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EXPLANATION OF FIGURES

FIG. 1. *Cystopage intercalaris;* drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. *A*, Portion of mycelial hypha with a captured specimen of *Plectus parvus;* invasion of the animal has been started by the intrusion of four haustorial branches. *B*, Portion of hypha with a captured specimen of *P. parvus* in a somewhat later stage of invasion. *C, D, E*, Portions of mycelial hyphae, each with a captured specimen of *P. parvus* that is invaded from head to tail by assimilative filaments. *F; G; H, a, b; I–Z:* Chlamydospores with adjacent portions of the hyphae bearing them; showing variations in size, in shape, and in manner of attachment of the reproductive bodies; and illustrating the distribution of septa in the empty hyphae, as well as the distribution of the perforated lumps of adhesive material that earlier had served in capture of nematodes.

FIG. 2. Sexual stage of a nematode-capturing fungus belonging in the Zoopagaceae; drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A*, Two intersecting mycelial hyphae, *a* and *b*, to each of which is attached an empty integument of a nematode referable apparently to *Acrobeloides bütschlii;* the two hyphae have put forth a pair of sexual branches which after fusing apically have produced a zygosporangium on a stalk arising from a position close to their junction. *B*, Two intersecting mycelial hyphae *a* and *b*, from which have been extended two pairs of sexual branches that after fusing have given rise to the two zygosporangia *c* and *d*. *C*, Two intersecting mycelial hyphae, *a* and *b*, from which have been extended a pair of intervolved sexual branches; these branches, after fusing apically, have given rise laterally to a zygosporangium about 15 μ below their junction. *D*, A mature or nearly mature zygospore surrounded by an irregularly thickened zygosporangial envelope. (For the sake of clearness the sexual branches are further shown, in whole or in part, without stippling, in supplementary drawings enclosed by broken lines; the small letters by which they are designated in these drawings correspond to the letters designating the parent hyphae.)

FIG. 3. Drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout.

A–M, *Cochlonema pumilum*: *A*, Small specimen of host animal, *Euglypha levis*, within which is contained a small thallus of the parasite that has devoted all its contents to the production of conidial apparatus; a few conidia are shown, some attached, others detached. *B*, A small specimen of *E. levis* within which a mature zygospore is shown attached to the membranous envelope of the small thallus that gave rise to it. *C*, A large specimen of *E. levis* within which is contained, besides three ungerminated supernumerary conidia, a well developed thallus of the parasite. *D*, A large specimen of *E. levis*, containing a thallus whose entire contents have migrated into the globose zygosporangium. *E, F, G*, Specimens of *E. levis*, each containing a thallus from which protoplasmic materials are still migrating into an enlarging zygosporangium. *H, I, J*, Large specimens of *E. levis*, each containing a nearly mature zygospore and the empty envelope of the thallus from which it originated. *K*, A large specimen of *E. levis* within which a zygosporangium is being formed apparently in a position between the proximal end of the thallus and the empty membrane of the parent conidium. *L, M*, Large

specimens of *E. levis*, each containing a fully mature zygospore and the empty envelope of the thallus from which the zygospore originated.

N–P, Cochlonema ovolum: *N, O,* Two empty testae of *Sphenoderia dentata*, each containing the empty membranous envelope of a thallus whose protoplasmic contents went into the production of conidial apparatus. *P*, Detached conidia, showing usual variation in size and in shape.

Q–U, Stylopage minutula: *Q*, A mycelial hypha from which a dichotomously branched haustorium has grown into a captured amoeba, *a*; the hypha has further given rise to a conidiophore, *b*, bearing a conidium, *c*. *R*, Portion of mycelial hypha which has given rise to a young conidiophore, *a*, and to a somewhat older conidiophore, *b*, whereon two conidia, *c* and *d*, have been produced successively. *S*, Detached conidia, showing usual variation in size and in shape. *T, U,* Germinating conidia.

FIG. 4. *Acaulopage dichotoma;* drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. *A*, Portion of mycelium to which are attached six captured amoebae, *a–g*. *B–E,* Portions of hyphae, to each of which is attached a captured amoeba. *F, G,* Portions of mycelium, each bearing a conidium in an early stage of development. *H–S,* Detached conidia, showing usual variations in respect to size and manner of branching, as well as in respect to number and length of the empty membranous appendages.

NOTES ON THE GEOGLOSSACEAE OF BERMUDA

J. M. Waterston, J. W. Sinden and H. H. Whetzel

(with 1 figure)

The Geoglossaceae are well represented in Bermuda by some four genera and seven or eight species. The following notes are based on collections made over a period of seventy years. The earliest collection was that by H. N. Moseley, Naturalist of the British Challenger Expedition, in 1873. Berkeley (1, 2) published two lists of Bermuda fungi based on Moseley's collections which were later revised by M. C. Cooke and published by Hemsley (5). Only one species, *Trichoglossum hirsutum* (Pers.) Boud. (recorded as *Geoglossum hirsutum* Pers.), was reported.

Extensive collections of fungi were made both by Dr. B. O. Dodge in 1911 and by Dr. F. J. Seaver in 1912. A list of these, together with some additional species collected by Dr. Stewardson Brown and Dr. N. L. Britton, was published by Seaver (6, 7). These collections added *Geoglossum nigritum* Cooke and *Trichoglossum hirsutum f. Wrightii* Durand to the list. The latter was raised to specific rank by Durand (4) after an examination of Bermuda material and named *Trichoglossum Wrightii* Durand. A further record, *Geoglossum pumilum* Winter, was added by Durand (4) and was later noted by Seaver (8).

Further collections were made by H. H. Whetzel during the years 1921 and 1922, whilst acting as the first plant pathologist appointed to the Bermuda Department of Agriculture. Additional collecting was done by Lawrence Ogilvie, appointed plant pathologist in 1923, in coöperation with the junior author and with Dr. F. J. Seaver who revisited the Colony in 1926.

Dr. Seaver revisited Bermuda on two further occasions during the autumns of 1938 and 1940 and, in company with the senior author, made further collections of fungi.

Over thirty separate collections of Geoglossaceae are listed from Bermuda in the Herbarium of the Department of Plant

Pathology at Cornell University. Most of the specimens have been collected during the winter months (November to February) when climatic conditions appear to be most favorable. The weather experienced during this period is usually cool (55°–65° F.) and the monthly rainfall is a little over four inches. The mean relative humidity during this period ranges from 76–78% and the number of hours of sunshine per day ranges from 5.5 to 6.6 in comparison with from 6.4 to 9.6 of the summer months.

Bermuda's soil is derived from aeolian limestone of recent geological age and as a result is uniformly calcareous with a pH ranging from 7.5 to 7.8. The topography is hilly with local broad valleys occupied by fresh water or brackish marshes. Damp pockets of soil in these rocky hillsides, as well as on lower ground, form ideal habitats for species of Geoglossaceae.

Recorded below are two species of *Trichoglossum*, three or possibly four species of *Geoglossum*, one species of *Gloeoglossum* and a species of *Mitrula* new to science. New Bermuda records are designated with an asterisk. One of us (J. W. S.) is responsible for making most of the determinations. Unless otherwise stated, the numbers attached to the collections refer to the accession number in the Herbarium of the Department of Plant Pathology, Cornell University.

TRICHOGLOSSUM HIRSUTUM (Pers.) Boud.

This species was first collected by Moseley in 1873 on dead *Sphagnum* under ferns in Devonshire Marsh. The record was reported by Berkeley (1, 2) as *Geoglossum hirsutum* Pers. and also by Hemsley (5). Seaver (6) searched the same station diligently in 1916 and states he was unable to duplicate the collection. Four collections were subsequently made: Whetzel, Nov. 1921–Feb. 1922, *33200*, *33209;* Whetzel, Seaver and Ogilvie, Jan. 1926, *33192*, *33193*.

Habitat: On soil in Paget Marsh in association with *Geoglossum fallax* Durand and in Walsingham.

TRICHOGLOSSUM WRIGHTII Durand.

This was first listed by Durand (3) as a form of *Trichoglossum hirsutum* based on two specimens from Cuba. It was later raised

to specific rank by Durand (4) after examination of Bermuda material collected Nov. 29–Dec. 14, 1912 (Britton, Brown and Seaver, *1404*). Bermuda material was also examined by Sinden and Fitzpatrick (10) in a critical review of the genus.

This species is one of the commonest collected in Bermuda. Whetzel, Jan. 20, 1922, *33201;* Whetzel, Seaver and Ogilvie, Jan. 1926, *33183*, *33185*, *33189*, *33190*, *33194;* Seaver and Waterston (9), Nov. 28–Dec. 14, 1938 (N. Y. B. G. *178*).

Habitat: Among crab grass, *Stenotaphrum secundatum* (Walt.) Kuntze, "Fruitlands" and "Argyll" in Warwick, Agricultural Station, Walsingham, "Harrington House."

GEOGLOSSUM NIGRITUM Cooke.

This species was first reported by Seaver (6) who found it abundant on rocky hillsides among mosses (Nov. 29–Dec. 14, 1912). It is another very common species and is represented by ten separate collections in the Cornell University Herbarium: Whetzel, Dec. 1921, *33207;* Whetzel, Feb. 1922, *33208;* Whetzel, Seaver and Ogilvie, Jan.–Feb. 1926, *33184*, *33186*, *33187*, *33188*, *33191*, *33195*, *33197*, *33198*.

Habitat: Rocky hillsides among mosses.

*GEOGLOSSUM FALLAX Durand.

This species is represented by two collections: Whetzel, Jan. 1922, *33204;* Whetzel, Seaver and Ogilvie, Jan. 1926, *33203*.

Habitat: Found in association with *Trichoglossum hirsutum* (Pers.) Boud. on soil in Paget Marsh.

*GEOGLOSSUM PYGMAEUM Gerard.

There are three collections of this species: Whetzel, Jan. 1922, *33205*, *33210;* Whetzel, Seaver and Ogilvie, Jan. 1926, *33206*.

Habitat: Found in association with *Geoglossum nigritum* Cooke in Walsingham.

GEOGLOSSUM PUMILUM Winter.

A single collection by Ogilvie was taken on Jan. 26, 1926, *33218*, in Walsingham. There is one other record of this species in Bermuda collected by Britton, Brown and Seaver, Nov. 29–Dec. 14, 1912 (N. Y. B. G. *1364*). Durand (4) records the posi-

tion of this species as "closely allied to *G. pygmaeum* Ger.". He adds, "I have not seen Winter's type, so that the identification depends upon the description only."

Habitat: Damp soil in woods.

*GLOEOGLOSSUM GLUTINOSUM (Pers.) Durand.

There are three collections of this interesting species: Whetzel, Jan. 1922, *33199*, *33202;* Whetzel, Seaver and Ogilvie, Jan. 1926, *33196*.

Habitat: Soil among grasses in Walsingham.

***Mitrula bermudiana** Waterston, sp. nov. (FIG. 1)

Plants small, solitary, slender, 1 cm. high; ascigerous portion distinct from stem below, 5 mm. long, 2 mm. broad, 0.5 mm. thick, hygrophanous tan in color; stem equal.

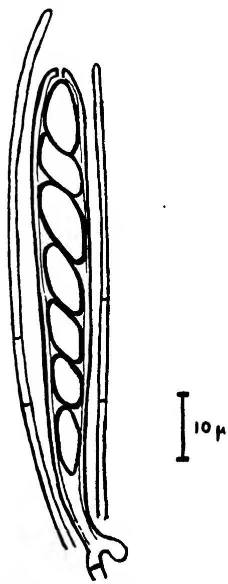

FIG. 1. *Mitrula bermudiana*, ascus and paraphyses.

Asci clavate, apex narrowed, the pore blue with iodine, 81–105 × 6–9 μ, mean 90 × 6 μ; spores 8, obliquely uniseriate, hyaline, guttulate, continuous, smooth, ellipsoid, 9–15 × 3–4 μ, mean 12 × 3 μ; paraphyses hyaline, filiform, 2 μ thick, simple, with few septa.

Ascomatibus minutis, solitariis, 1 cm. alt.; clavis a stipite distinctis 5 mm. long., 2 mm. diam., pallide brunneis; ascis clavatis apice attenuatis, jodo caerulescentibus; 81–105 × 6–9 μ 8-sporis; sporis monostichis, hyalinis, ellipsoideis, levibus, 9–15 × 3–4 μ; paraphysibus hyalinis, filiformibus, saepe septatis, 2 μ diam.

Habitat: Type collected in soil among rocks on hill top, Walsingham, Jan. 20, 1926, by H. H. Whetzel, *33212*. An earlier collection by Whetzel from a grassy hillside at Walsingham, on Jan. 20, 1922, *33211*, proved immature. Type deposited in Plant Pathology Herbarium, Cornell University, Ithaca, N. Y., as No. *33212*.

The non-septate, ellipsoid, uniseriate spores distinguish this species from all those previously described by Durand (3) from North America which are characterized by the presence of paraphyses in the ascoma. No records of this genus have hitherto been recorded from Bermuda.

DEPARTMENT OF PLANT PATHOLOGY,
CORNELL UNIVERSITY,
ITHACA, NEW YORK
AND
DEPARTMENT OF AGRICULTURE,
PAGET EAST,
BERMUDA

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THE FUNGUS CAUSING ZONATE LEAFSPOT OF COWPEA

C. L. Lefebvre and J. A. Stevenson [1]

(with 2 figures)

A disease of cowpea (*Vigna sinensis* (L.) Endl.), which has been designated here as the zonate leafspot (fig. 1, *A–B*), was much in evidence, particularly in the Southern States during the 1943 growing season. The disease has been known for many years as a minor trouble of cowpea and the causal organism has been called *Amerosporium oeconomicum* Ellis & Tracy. One finds, however, that the fungus causing this leafspot has septate conidia, hence it does not agree with the description given by Ellis and Tracy (**9**, p. 102), and should not be referred to the genus *Amerosporium*. Because this leafspot of cowpea is so striking, many collectors have referred their specimens to *Amerosporium*, however, probably without a microscopic examination of the causal fungus. Since the leafspot is common, apparently wherever cowpeas are grown, and since so many have either wrongly identified the causal fungus or left their specimens undetermined, as indicated by the number being sent in for identification, both the disease and the causal organism appear to warrant further study.

HISTORY AND DISTRIBUTION

Ellis and Tracy (**9**) in 1888 described *Amerosporium oeconomicum* as a new species, producing orbicular spots, 2–6 mm. in diameter, on leaves of "cowpea," at Starkville, Mississippi. Ellis and Everhart issued the same fungus on "*Dolichos arvensis*" as

[1] Pathologist, Division of Forage Crops and Diseases, and Senior Mycologist, Division of Mycology and Disease Survey, respectively, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture. The authors are indebted to P. L. Ricker, Division of Forage Crops and Diseases, for making the photographs used to illustrate this paper.

No. *2574* .(1891–92) in their exsiccati *North American Fungi*, under the name *Amerosporium Dolichi* Ellis & Ev., but without a description, hence a nomen nudum. Farlow (**11**, p. 211) points this out by saying "The name *Amerosporium oeconomicum* and *A. Dolichi* are founded on material of the same host, locality, and collector, and J. B. Ellis states in a letter that they are synonyms."

Later Tracy and Earle (**24**, p. 112) repeated the original description, giving the host as *Dolichos sinensis* and adding Biloxi, Miss., as an additional locality. Atkinson (**3**, p. 33) cited collections by himself and Duggar at Auburn, Ala. Underwood and Earle (**25**, p. 175) and Earle in Mohr's Plant Life of Alabama (**12**, p. 261) repeated Atkinson's citation, changing the host designation to *Vigna catjang*. North Carolina was added to the area of occurrence by Stevens and Hall (**21**), who compared the symptoms produced by *Amerosporium* with those caused by *Cercospora Dolichi*, noting that the former at times caused defoliation.

The fungus has been noted in Connecticut by Clinton (**6**), in Indiana by Osner (**13**), and attracted some attention during a number of years in Delaware (**1, 2**). Only one report of the occurrence of the fungus outside of the United States has been found. Faris (**10**) found it in the Dominican Republic in 1923 and the record was later included by Ciferri (**4**) in his comprehensive account of the fungi of that country. The files of the Plant Disease Survey indicate its presence also in Arkansas, Florida, Georgia, South Carolina, and Virginia.

Spegazzini's genus *Amerosporium* was described (**19**, p. 20) with non-septate conidia and the several species assigned to it by other mycologists have conformed, except in the case of *A. oeconomicum*. Petrak and Sydow (**16, 17**) investigated the type species and certain other members of the genus at some length and decided that it could properly be retained with certain emendations. They made no mention of Ellis and Tracy's species.

FIG. 1. *Aristastoma oeconomicum* on cowpea; *A*, infected leaf showing 3 lesions, bearing pycnidia and alternating zones of brown and white tissue. At right, lesion has dropped out resulting in a "shot hole" effect. Solid brown lesion at left center caused by *Cercospora Dolichi* Ellis & Ev., × 1; *B*, single lesion with irregularly arranged pycnidia, × 8.

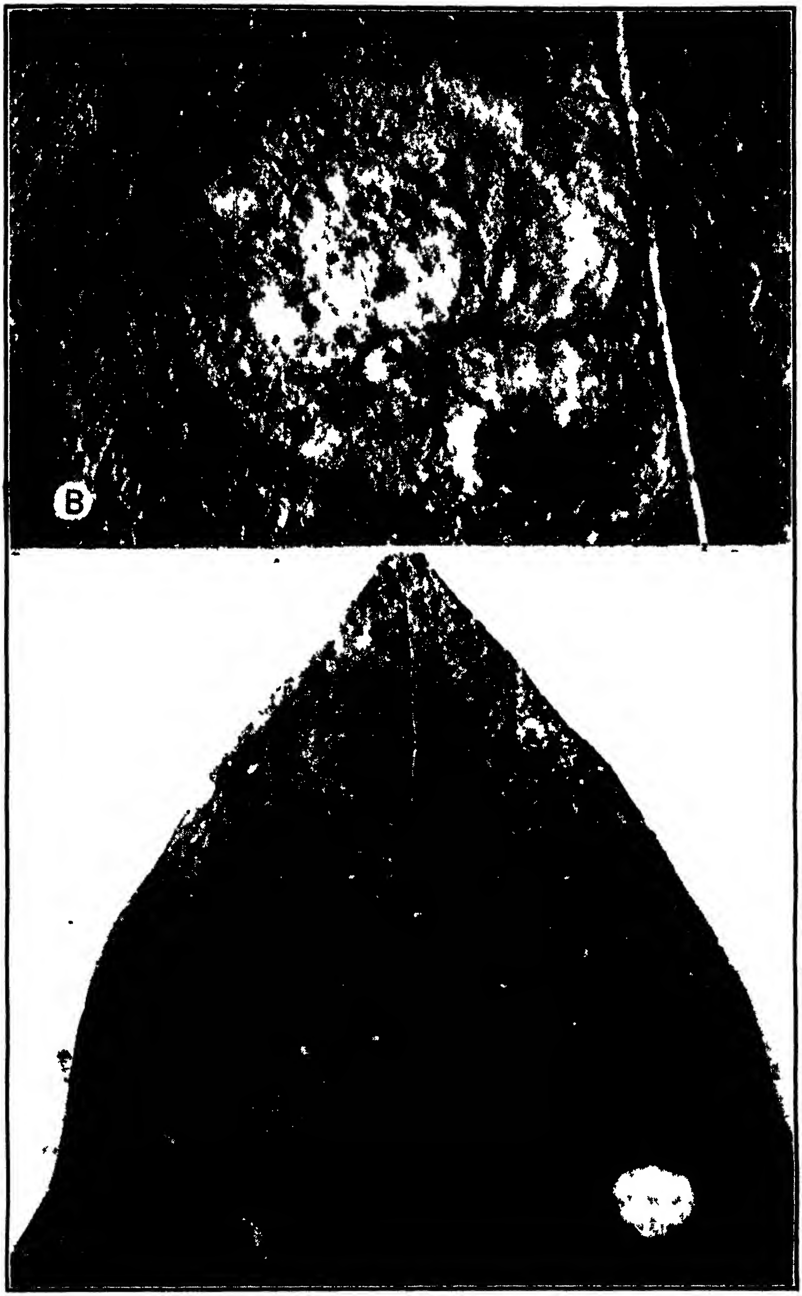

FIG 1.

It is evident, of course, that Ellis and Tracy, in placing their species in *Amerosporium*, overlooked the fact that the conidia are septate—if not at first, certainly at maturity. These authors merely recorded them as "nucleate." Clinton (**6**) appears to have been the first to observe the septate condition, commenting that:

"This exsiccati specimen (Ellis and Everhart, No. Amer. Fungi, No. *2574*) plainly shows that the spores are septate (about three septate when old), and the specimens collected in Connecticut also indicate that they would become septate with age. This may mean that the fungus belongs in a different genus, since the spores of *Amerosporium* are said to be continuous."

Tehon (**23**, p. 445) also noted the septate condition of the conidia, since in discussing his newly described species, *Chaetoseptoria Vignae*, he says, "In its external aspect this fungus is similar to that of Tracy and Earle's incorrectly placed *Amerosporium oeconomicum*, which attacks the same host."

Present studies have definitely confirmed the presence of septate conidia which makes it necessary to reassign the fungus generically. A search of the literature suggests the possibility of placing this cowpea fungus in one of four genera, *Chaetosticta*, *Trotteria*, *Dasypyrena*, or *Aristastoma*.

The genus *Chaetosticta* was established by Petrak and Sydow (**15**) to care for *Chaetomella perforata* Ellis & Ev. (**8**) which they pointed out could not properly be included in *Chaetomella*. Ellis (**7**), however, later found this fungus to be an ascomycete and renamed it *Venturia occidentalis* Ellis & Ev., which Saccardo transferred to *Acanthostigma occidentale* (Ellis & Ev.) Sacc. The genus *Chaetosticta* was described as having superficial pycnidia, sparingly clothed with straight, black, continuous bristle-like hairs, more thickly set around the ostiole. These characteristics, contrasted with the imbedded pycnidia and the single ring of setae around the ostiole as noted hereafter for the cowpea fungus, to say nothing of the fact that apparently an ascomycete is involved, appear sufficient to eliminate *Chaetosticta* from further consideration.

Trotteria was described by Saccardo (**18**) as having superficial, hypophyllous fruiting bodies clothed with septate, brown setae. Portions of the type collections of Saccardo's two species were examined and confirmed his general characterization, which effectively removes *Trotteria* from the discussion as a possible generic designation for a fungus with imbedded pycnidia.

Clements and Shear (**5**) consider *Chaetosticta* and *Trotteria* synonymous with *Dasypyrena*, which was originally described by Spegazzini (**20**) and accepted by v. Hoehnel (**26**). Petrak (**14**) and Petrak and Sydow (**15**), however, have pointed out that Spegazzini's fungus is a Pyrenomycete, which in turn disposes of *Dasypyrena*.

Tehon (**22**) described the genus *Aristastoma*, typified by *A. concentrica* on *Vigna sinensis*, in 1933 and his description fits in all particulars the cowpea fungus, which we are considering. He notes particularly imbedded pycnidia with a comparatively wide mouth, surrounded by a ring of septate setae and 1–4-septate conidia. However, the erecting of a new genus and species by Tehon did not help clear up the tangled nomenclature because he did not consider Ellis and Tracy's *Amerosporium oeconomicum*, described in 1888 as the cause of the leafspot of cowpea in question.

SYMPTOMS OF THE DISEASE

The symptoms of the leafspot on cowpea are essentially as described by Ellis and Tracy (**9**) and by Tehon (**22**). There appears to be greater variation, however, in the size of the spots than was mentioned by them, because we find lesions measuring up to 16 mm. in diameter (FIG. 1, *A*). Spots are usually more or less circular, but they may coalesce and become quite irregular. Also, we find that as the fungus develops in a lesion the tissue becomes papery and brittle, resulting in the dropping out of the whole lesion, producing a "shot hole" effect (FIG. 1, *A*). The pycnidia are mostly produced in this white, papery center of the lesions (FIG. 1, *B*), but they are sometimes found extending beyond this region in the brownish-red tissue forming the outer portion of the spots.

MORPHOLOGY AND NOMENCLATURE OF THE FUNGUS

Pycnidia are usually spherical (FIG. 2, *A*), erumpent, epiphyllous; the 10 measured ranging from 155–260 μ, averaging 208 μ; ostiole circular, 15–30 μ, averaging 23 μ, surrounded by a ring of more or less upright setae, these blackish-brown at the base, becoming lighter toward the tip, 0–6 septate, straight, 30–170 μ long by 6–15 μ wide. The setae are usually broken in packets if the specimens have been handled roughly and may, therefore, appear rather blunt upon examination. Conidia are rather pointed, oblong, 1–7, mostly 3-septate, but in immature pycnidia many conidia are non-septate; 16–42 by 4–6 μ, averaging 26.0 by 4.7 μ. Conidia from different pycnidia may differ quite widely (FIG. 2, *C–D*) even though mounts are made from the same leaf. The fungus was found to grow readily in pure culture and single-conidium isolations have been used in the present study.

The above measurements of the various fruiting structures are those for the specimens that were examined by the writers, while the measurements in the description of the new combination that follows differ slightly, since they are the over-all measurements, including those of other investigators.

Since the fungus under discussion has septate conidia, it is obvious it does not belong in the genus *Amerosporium* which is characterized by species having non-septate conidia. It seems apparent, however, that the cowpea fungus can be properly referred to the genus *Aristastoma*, but that a new combination becomes necessary, inasmuch as the specific epithet of Ellis and Tracy has priority.

Aristastoma oeconomicum (Ellis & Tracy) Tehon,[2] comb. nov.

Syn. *Amerosporium oeconomicum* Ellis & Tracy in Ellis & Ev. Jour. Myc. **4**: 102. 1888.

[2] We credit the combination to Dr. L. R. Tehon with his permission on the basis of his use of the binomial on one of the herbarium specimens of the fungus that he kindly loaned us for study.

FIG. 2. *Aristastoma oeconomicum*. *A*, pycnidium with ostiole surrounded by setae, × 280; *B*, setae, showing septa, and tapering to fairly acuminate tips, × 600; *C*, conidia with a larger proportion than usual showing more than 3 septa, × 600; *D*, conidia showing many with fewer than 3 septa, probably from an immature pycnidium, × 600.

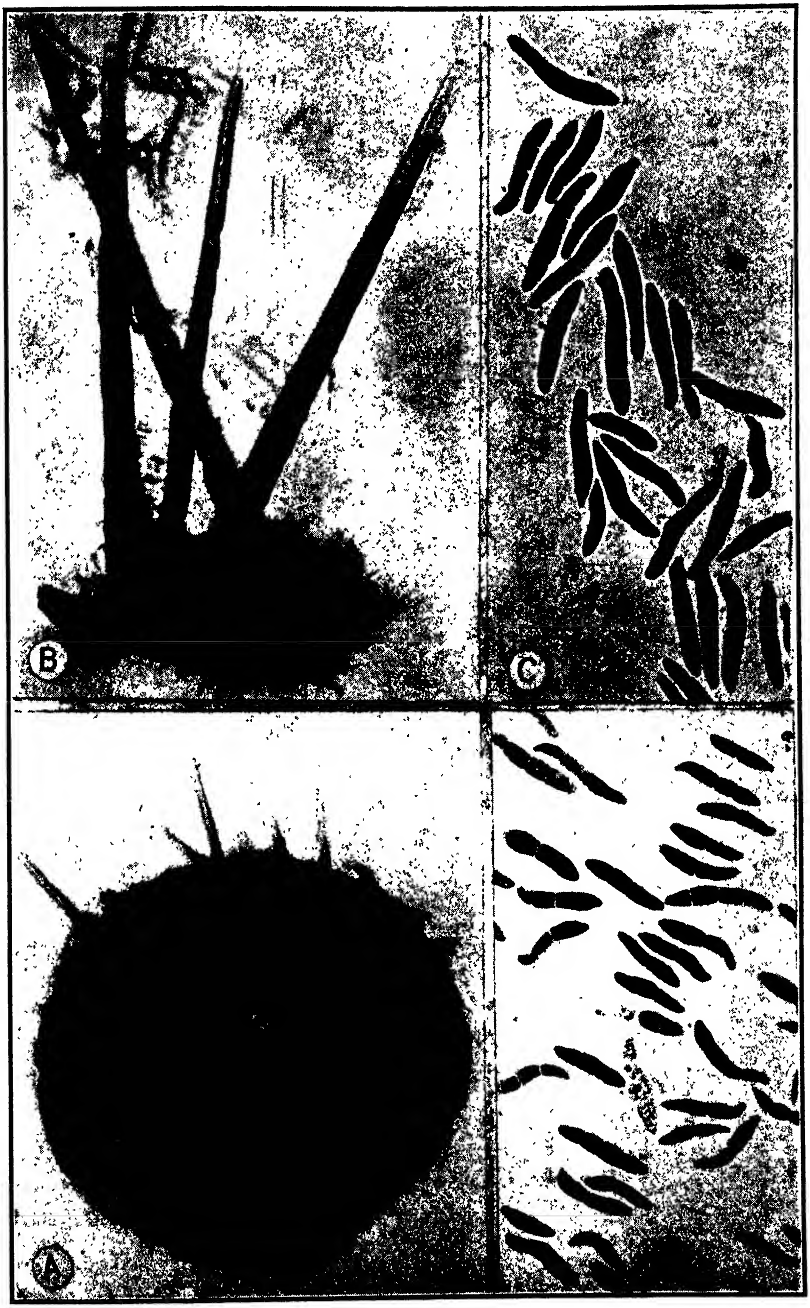

FIG. 2.

Aristastoma concentrica Tehon, Mycologia **25**: 248–249. 1933.

Folicole, causing circular to irregular spots 2–16 mm. in diameter, these marked more conspicuously above than below by alternating concentric zones of brownish-red and white tissue, the margin brownish-red, sometimes affected tissue dropping out causing a "shot hole" effect; pycnidia spherical to applanate, arranged irregularly, usually in white zone of spots only, but sometimes extending into brownish tissue, erumpent, epiphyllously only, membranaceous except near the ostiole, 155–270 μ in diameter, ostiole circular, 15–35 μ in diameter, crowned by a ring of more or less upright setae, these blackish-brown at base, becoming lighter toward the apex, 0–6-septate, pointed, straight, 20–170 μ long by 6–15 μ wide; conidia oblong, 0–7, mostly 3-septate, 15–42 $\times$ 4–6 μ.

On leaves of *Vigna sinensis* (L.) Endl., Illinois (Tehon No. *5453* type), Alabama, Arkansas, Delaware, Florida, Georgia, Indiana, Mississippi, North Carolina, South Carolina, Virginia; *Phaseolus* sp., Biloxi, Miss.; *Phaseolus angularis*, Arlington, Va.; *Phaseolus Max*, Arlington, Va.; *Phaseolus radiatus*, Arlington, Va.; *Phaseolus vulgaris*, Brunswick, Ga. As noted previously, reports of the species on *Dolichos* spp. and *Vigna catjang* are properly *Vigna sinensis*, cowpea.

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NOTES ON THE PILEATE HYDNUMS

Walter H. Snell

Precisely why one who can think of enough problems in the *Boleti* to last him for at least 25 years should ask for more trouble by becoming interested in the hydnums, may be somewhat difficult to explain. None but a few species of *Boleti* are at all abundant and one can collect for years to find that he has seen single specimens of most species only a very few times. The hydnums occur even less commonly. Banker (1, pp. 99–100) after years of study of this group spoke in a disappointed manner of the "lack . . . of getting suitable material," "the local character of the distribution of these plants," "the comparative rarity with which they are found," the intermittence of their appearance.

The fact is, however, that as is the case with the *Boleti*, the pileate hydnums have long fascinated me for some unexplainable reason and similarly the difficulties involved in the identification and identity of specimens provide a stimulating challenge. Also, the hydnums are to be found in the same habitats as the *Boleti* and their collection therefore involves no extra or different effort in the hunting. Furthermore, whereas the study of the *Boleti* has become a rather intense preoccupation for a good part of the time available, if not actually at times a sort of mycological Old Man of the Sea, the hydnums have been a diversion and have provided mental refreshment.

Therefore, it is hoped that at odd times some contribution can be made to our knowledge of this rather generally neglected group of fungi.

Calodon geogenius (Fries) Quél.

Until very recently, this species was all but unknown on this continent, at least as far as I am aware of publications on the subject. In 1886, Peck (10, p. 43) had reported it from South

Balston, New York, and Banker, who had included it in a list of "Species Dubiae et Inquirendae" (**1**, p. 135), later verified it in 1913 (**3**, p. 204). In 1940, Wehmeyer (**12**, p. 100) reported it in Nova Scotia and in 1942, Coker (**9**, p. 94) reported it from Georgia near the South Carolina line. Finally, it was reported as collected by Henry A. C. Jackson and myself in County L'Islet, Quebec, following the 1941 Foray (**11**, p. 666—incidentally, with the specific name not in generic agreement).

As far as the records go, therefore, this species is very rare and very "spotty" in occurrence. Like several other species of the pileate Hydnaceae, it is at present known only from the northern and southern ends of the Appalachian system. This is probably only because of the fortuitousness of the collecting of these fungi, although it must be remarked that the eastern part of the United States has certainly been more carefully searched than contiguous portions of Canada.

The records make no mention of the abundance of this species in the few cases reported and one is left with the impression that it does not fruit often or in a prolific manner. In the proper places, however, it can be not uncommon or sparse. Jackson has found it in three patches of woods near St. Aubert, County L'Islet, Quebec. In one patch of woods which provides especially good hydnum collecting, he has collected it every year for the past six years and it has been abundant to very abundant when it was at all moist.

The records of the habitat of this species are not precise as to desired details. Peck merely said "woods" and Coker mentions only the deep humus on the bank of a creek. Wehmeyer is somewhat more specific, for he says "Under conifers." At the St. Aubert locations in the province of Quebec where Jackson and I found it, it has occurred under coast white cedar or cedar and spruces. We did not make any effort to determine with which of these trees the mycelium was connected.

Coker's description and photographs indicate that in the southern extremity of the range, pilei are more likely to be single, simple, plainly stipitate and gregarious, although he says that they are often confluent and complicated. Wehmeyer, on the

other hand, emphasizes the squat, complicated and almost sessile characters of the fructifications with fused stems. It is thus that Jackson and I have found it, and even more pronouncedly so. The fructifications often have no determinable stipes but are fused, concrescent, almost amorphous masses, sometimes as if they grew out of an irregular, straggling fissure in the soil, and they are long-obconic in section the short way and scarcely flaring. In fact, I have rarely seen single stipitate specimens with a regular pileus.

Coker and Wehmeyer emphasize the darker colors which this species shows—pale to deep wood-brown to dark olive-brown to olive-black, with olive-yellow tints, of course with very light to bright sulphur-yellow margin. Possibly I may have found much younger or fresher specimens but the colors have been much lighter—sulphur-yellow to fuscescent or grayish-ochraceous, with tinges of yellowish or deep olive-buff.

I find the spores wood-brown to army-brown in deposit, pale yellowish under the microscope and 3.5–5 × 3–4 μ, or essentially as given by Coker and Wehmeyer, except that Wehmeyer's measurements are slightly smaller.

CALODON FERRUGIPES AND HYDNUM BREVIPES

These two species are additional examples of the distributional situation mentioned in connection with *Calodon geogenius*—being known, in the literature at least, only from widely separated points and at extremes of a known range. These species were both described by Coker from North Carolina. *C. ferrugipes* was described as a *Hydnellum* in 1919 and was not reported again until 1938 from Manitoba by Bisby *et al.* (**5**, p. 80). It has been found in Florida by Murrill. In 1940, I collected it at Friendship, Maine.

Hydnum brevipes was described as a *Sarcodon* in 1939. In 1940, Jackson and I collected it near Elgin Road, County L'Islet, Quebec, and in 1941 I found it at Friendship, Maine. All three of these collections were identified by Dr. Coker.

In the generic arrangement preferred by me, these species should be **Calodon ferrugipes** (Coker) Snell, comb. nov. and **Hydnum brevipes** (Coker) Snell, comb. nov.

HYDNUM ROSEOLUM AND H. AMARESCENS

Banker in 1913 (**2**, p. 16) described the former species from specimens collected by Murrill and House in North Carolina as a small, pale rose-colored *Sarcodon*, without making mention of odor or taste. In 1926, Coker (**7**, pp. 274–275) included Banker's species in *H. amarescens* Quélet, but in 1939 (**8**, p. 375), with "good fresh specimens" at hand, he decided that "the two species can easily be separated by the mild taste, very thin flesh, much shorter spines and paler, more rosy color." He redescribed the species, still in the genus *Sarcodon*.

In 1942, Donald P. Rogers collected a roseate hydnum in Rhode Island, and whichever species it may prove to be, it is an interesting collection. If it should be *amarescens*, it would be the first time that it has been found on this continent, to my knowledge, except as confused with *roseolum*. If it is *roseolum*, here is another example of a rare species known only from two localities widely separated, north and south.

The possible identity and value of this specimen were not recognized at the time of collection and therefore its taste and some other features in the fresh condition were not noted although partial notes were made. Consequently, attempts made to identify it in the dried state are considerably handicapped. I am, however, unable to detect any bitterness of taste of the flesh and it would seem that this should not be difficult if the specimen is *amarescens*, since this species is supposed to be so acrid as to constrict the throat when tasted. Other bitter fungi, such as *H. fennicum* and *Boletus felleus*, are bitter enough to the taste when dry. Furthermore, the deep rosiness, especially of the flesh, and other characters appear to make the specimen fit the description of *roseolum* better than that of *amarescens* and therefore, I am calling it the former.

Banker and Coker give the width of the pileus as 3 or 4 cm. This specimen is 7 cm. broad. The pileus is also more glabrous, subtomentose only in spots and with only a slight tendency to be tomentose-squamulose. Also, the spines are up to 2 mm. long, although most of them are only 1 or 1.5 mm. long, somewhat longer than given by Banker and Coker, but still shorter than those of *amarescens*. Further, the spores in mass as found

in depressions on the stipe are definitely fawn-color instead of pale brown as given in other descriptions. Otherwise, the specimen seems to be in accord with the descriptions of *roseolum*, especially as to the stipe tapering downward to a greenish-blackish base and a somewhat radicating tip.

In the genus *Hydnum*, this species should be **H. roseolum** (Banker) Snell, comb. nov.

RHODE ISLAND SPECIES OF PILEATE HYDNUMS

Mycologically, Rhode Island has been more or less of a *terra incognita* at least as far as published data are concerned—from this point of view probably the poorest known political entity north of the Rio Grande, if not on the entire continent. The green plants of the State have been well known from the earliest times as a result of the studies of several well known botanists, but Bennett's publication of 1888 (**4**, pp. 76–94) contains the only list of fungi and was merely a start. Recent botanists in the State, if they had any interest at all in the fungi, were busy with pathological problems or, as in my own case, spent the bulk of the collecting season each year in other localities. It is not that the lack of data in Rhode Island makes much difference from any point of view, for the State is small and the bare spots on distribution maps are hardly noticeable. Further, the species found in Massachusetts and Connecticut are likely to be found in Rhode Island as well.

On the other hand, since it is rather generally the custom to designate distributional data by states, the mycobiota of the State of Rhode Island and Providence Plantations may as well be made known. Further, some facts of ecological importance may possibly be discovered, because there are certain features peculiar to Rhode Island besides its politics and its independence of point of view. Coniferous woods are not common in the State, more especially since the destruction of most of the white-pine stands in the 1938 hurricane, and the hardwoods are distressingly uniform in type for the most part. The higher fungi are not at all common. It is rather disconcerting even for an adopted Rhode Islander to notice that he comes across few of the larger fungi in his own state on excursion after excursion,

only to find that he begins to collect species in varying abundance as soon as he crosses the lines into Massachusetts and Connecticut. It has too often been remarked that the best way for a Rhode Islander to collect fungi is to go elsewhere.

Inasmuch as it will probably be some time before a preliminary list of Rhode Island fungi known to date can be prepared for publication, it may be of value to record here the pileate hydnums that have thus far been collected. They are as follows with those previously reported in Bennett's list (p. 81) marked with an asterisk: **Calodon aurantiacus* (Alb. & Schw. ex Batsch) Karsten; **C. cyaneotinctus** (Peck) Snell, comb. nov. (det. by W. C. Coker); ?*C. scrobiculatus* (Fries) Quélet; *C. velutinus* (Fries) Quél. (det. by D. P. Rogers, confirmed by W. C. Coker); **C. zonatus* (Batsch ex Fries) Quélet; **Dentinum albidum** (Peck) Snell, comb. nov.; **D. repandum* (L. ex Fries) S. F. Gray; *Hydnum cristatum* Bres.; *H. fennicum* Karsten; **H. imbricatum* L. ex Fries; *H. roseolum* (Banker) Snell; *Phellodon alboniger* (Peck) Banker; *P. amicus* (Quél.) Banker; *P. graveolens* (Delast.) Banker (det. by W. C. Coker); **Steccherinum adustum* (Schw.) Banker; **S. ochraceum* (Pers. ex Fries) S. F. Gray.

In addition, Bennett's list contains the following species which have not been reported since that time: *Hydnum ferrugineum* Fries [*Calodon ferrugineus* (Fries) Quélet], perhaps, if not probably, the same as *C. scrobiculatus; H. subsquamosum* Batsch ex Fries & Romell, which is supposed to be the same as *H. badium* Pers., considered by Bourdot and Galzin (**6**, pp. 448 & 449) to be distinct from *H. imbricatum; H. cyathiforme* Schaeff. which Banker (**1**, p. 171) thinks is the same as *Phellodon tomentosus* (L. ex Fries) Banker, although Bourdot and Galzin (**6**, pp. 462 & 463) keep the two distinct; and *H. Erinaceus* (Bull. ex Fries) Pers.

BROWN UNIVERSITY,
PROVIDENCE, R. I.

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NOTEWORTHY SPECIES OF LEPIOTA AND LACTARIA

Gertrude S. Burlingham

(with 7 figures)

The species of *Lepiota* described in this article were collected under Monterey Cypress trees (*Cupressus macrocarpa*) on Point Lobos which is located south of Carmel Bay in Monterey Co., California. My primary purpose in going to Point Lobos was to determine what species of *Russula* or *Lactaria* might be found growing in this habitat. However, throughout the season from October to May no species of either genus appeared. But there was an abundance of several species of *Lepiota* from February through April, most interesting of which were the following:

Lepiota cupressea sp. nov. (fig. 1; 6, *A*)

Pileus convex to plane, from 3.5 to 8 cm. broad; surface dry, minutely pruinose-downy at first becoming floccose to areolate outside the disc, warm sepia tone 1 with a livid tinge, to brownish-drab, becoming much paler over the marginal area as the cuticle breaks up; context quickly Etruscan red where wounded, as this disappears becoming raw umber, mild and sweet at first then slowly peppery, especially in the lamellae; margin white and minutely downy when young with the sterile edge projecting beyond the lamellae; lamellae white, fimbriate, staining first yellow then salmon, and finally sepia, free, somewhat remote, narrower at the inner end, appearing ventricose in mature specimens, unequal, a number forking near the inner end, broad, close; spores fleshy-white tone 1–2, ellipsoid, apiculate, uniguttulate, 7.5–9.5 $\mu \times$ 4.5–5 μ; stipe white, becoming reddish where wounded than raw umber tone 1, minutely fibrous to floccose, bulbous, rather firm becoming hollow, 5 cm. to 7.5 cm. by .8 to 1.5 cm. at the apex and from 1.5 to 2.2 cm. through the bulb; annulus superior white becoming red where bruised then sepia, darker on the edge, hanging down and flaring out at first, then collapsing on the stipe, easily coming off if moved, otherwise persisting until mature.

Pileo primo convexo deinde plano, ab sepia (305 t-1) ad brunneum-rufum colorem (302) margine pallescente, sicco, primo pruinoso, deinde floccoso-areolato extra discum; carne rubente, postea umbrina (301), primo miti et dulci, deinde tarde acri; margine albo et subtiliter pubescente; lamellis primo albis, postea cremeis, deinde salmonicis, postremum sepiosis, remotis, inaequalibus, nonnullis ad stipitem furcatis; sporis albidulis (9 t-1 to 2), ellipsoidis, uniguttulatis, 7.5–9.5 μ × 4.5–5 μ; stipite albo, rubescente cum vul-

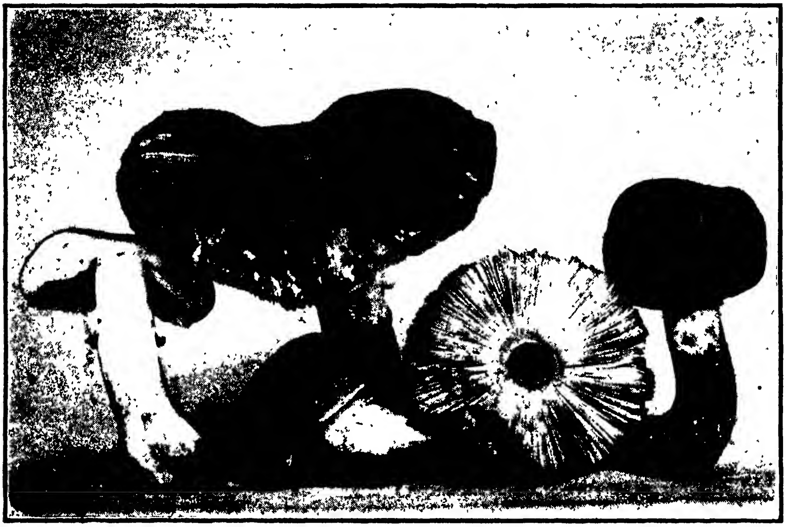


FIG. 1. *Lepiota cupressea* Burl. 4/5 nat. size.

neratus est, deinde umbrino, subtiliter fibrato-flocculoso, bulboso, firmo, postea cavo, 5–7.5 cm. × .8–1.5 cm. ad apicem, 1.5–2.2 cm. ad basim; annulo supero, albo, sed cum vulneratus est rubescente, deinde fuliginoso et fusciore margine, pendulo et persistente.

Type locality: Point Lobos, California. Type 9 Mar. 15–1937.

Habitat: On the ground under Monterey cypress trees.

Distribution: At various places on Point Lobos and at Pacific Grove and on the Seventeen Mile Drive on the Monterey Peninsula.

This species differs from *Lepiota brunnescens* Peck in the change of wounds to red before becoming sepia and in the final peppery taste, bulbous stipe, and the size and shape of the spores and easily removable annulus. From *Lepiota americana* it differs in the surface covering of the pileus and the peppery taste; from

Lepiota Badhami in the larger spores and lack of odor, and the pendulous annulus

Lepiota marginata sp nov (FIG 2 6, *B*)

Pileus broadly convex becoming plane to slightly centrally depressed, tinted incarnate to pale reddish lilac with center brownish drab tone 1, surface minutely floccose over a white background, center remaining well covered with the cuticle, very slightly viscid when wet, 4 to 5 7 cm broad, context white,

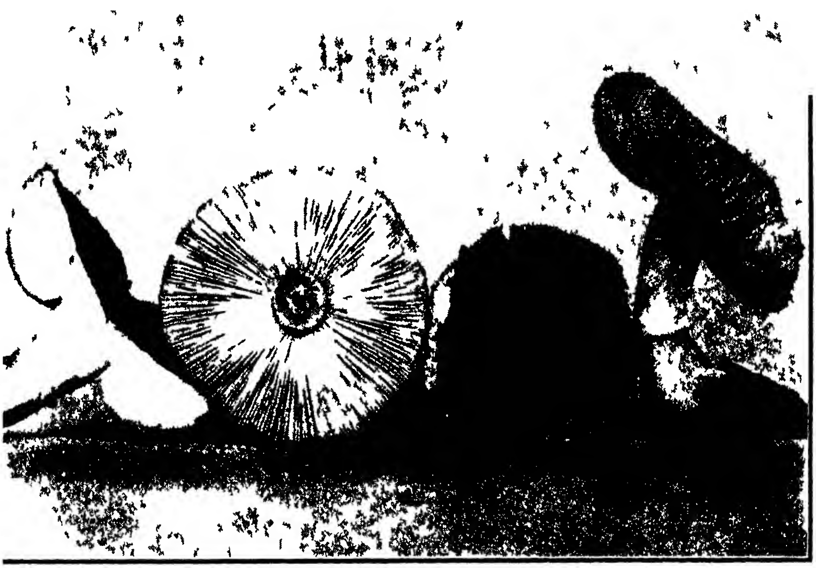


FIG 2 *Lepiota marginata* Burl

unchanging, taste good, odor none, lamellae white unchanging, free but not remote, broad, ventricose, minutely notched on the edge, unequal, spores white, uniguttulate, 4 3–5 3 $\mu \times$ 6 25–7 5 μ, stipe white above the annulus, becoming snuff brown to burnt umber below the annulus, pruinose to floccose at the apex, a little enlarged below, becoming hollow, 3 to 5 cm $\times$ 1 cm at the apex to 1 to 1 5 cm through the base, annulus white with brownish drab to incarnate edge, median to slightly superior, hanging down close to the stipe with the lower edge flaring somewhat, 3 to 6 mm broad, becoming movable and sometimes coming off

Pileo primo late convexo, deinde plano aut in centro subdepresso, incarnato et in centro brunneo-rufo (302 t 1), minute floccoso sed centro cuticula integra velato, viscidulo cum udus est, 4–5 7 cm lato, carne alba, immutabili, sapore

grato, inodora; lamellis albis, liberis sed non remotis, ventricosis, minute serratis; sporis albis, 4.3–5.3 $\mu \times$ 6.25–7.5 μ; stipite albo supra annulum, brunnescente infra annulum, pruinoso-floccoso ad apicem, dilatato infra apicem, postea cavo, 3–5 cm. × 1–1.5 cm.; annulo aut medio aut aliquantulum supero, rubro-brunneo (302) aut incarnato margine, pendulo, 3–6 mm. lato.

Type locality: Point Lobos, California.

Habitat: On the ground under Monterey cypress trees.

This species differs from *Lepiota rubrotinctoides* Murrill in the larger spores, the slightly viscid pileus and the annulus having an incarnate to brownish drab edge. The stipe below the annulus, the viscidity, and the annulus also distinguish it from *Lepiota decorata* Zeller. The specific name refers to the dark marginal line on the edge of the annulus. In well dried specimens there is a dark line at the apex of the stipe at the junction with the lamellae. The type species is number 13 April 10–1937, part of which is deposited in the herbarium of the Oregon State Agricultural College at Corvallis, and part in my herbarium.

Another species which occurred frequently is apparently close to *Lepiota decorata* Zeller and may be considered a dwarf form of that species. The pileus which varied from 3.5 to 6.5 cm. broad is densely pruinose over the center becoming floccose to minutely areolate outside the disc. When growing it is a beautiful vinaceous color fading to slate violet, but in drying the color disappears and the pileus becomes otter brown over the center and snuff brown over the remainder. The context is white and unchanging, mild and good in taste. The lamellae which are pure white, free, not remote, unequal and rarely forked become chamois color in drying. The edges are fimbriate and specimens of *Lepiota decorata* sent to me by Dr. Zeller also seem to have similar lamellae. The stipe which varies from 3 cm. to 5 cm. × .7–1 cm. at the apex to 1.5 cm. at the base is lilac floccose over the white surface. The annulus varies from median to slightly inferior or superior, flares out with the lower edge attached, and is white and ribbed on the upper side, slate violet and downy on the under side, and becomes movable. The photograph, figure 3, is natural size. A spore drawing is shown in figure 6, *C*.

The species of *Lactaria* which are described were collected in Orange and Seminole counties in Florida. The distribution of

Lactaria flocculosaceps however is known to extend from Florida to Vermont.

Lactaria fumeacolor sp. nov. (FIG. 4; 6, *D*)

Pileus fleshy, convex, centrally depressed, finally infundibuliform with extreme white-pruinose edge inrolled for some time, up to 12 cm. broad; surface fumosus to otter brown with some faint buff tone 1 to putty color in the center, or sometimes fading to that color, azonate to faintly zoned, glabrous, very viscid with

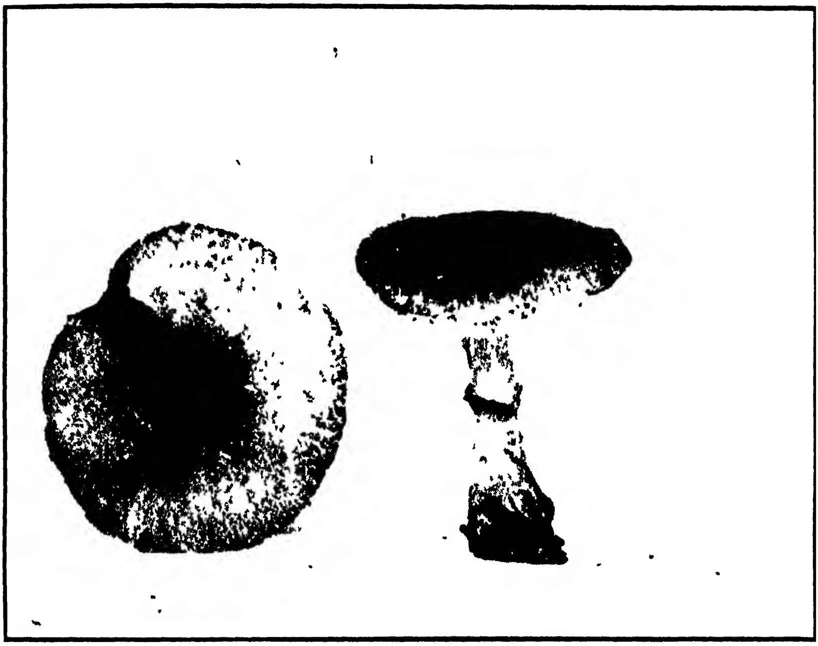


FIG. 3. *Lepiota decorata* Zell.

the cuticle separable on the margin which is entire; context white staining snuff brown to raw umber from the latex, without special odor; latex white slowly staining wounds, especially on the lamellae, first snuff brown then raw umber tone 4, slowly very peppery; lamellae fleshy-white to putty color, staining raw umber where injured, unequal, mostly simple, close, narrowed at the inner end and somewhat decurrent; stipe fleshy-white tone 4 to putty color, a little viscid, equal, 1.5–2.5 cm. × 5–8 cm.; spores maize yellow tone 2, coarsely echinulate and reticulate banded, 8.75–10.62 μ × 11.25–11.87 μ including the spines.

Pileo e late convexo expanso et infundibuliformi, 6–13 cm. lato, fumoso aut in disco pallidiore (311), azono aut interdum leviter zonato, viscidissimo, glabro; carne alba, brunnescenti cum vulnerata est (303–301), inodora; lacte albo, umbrino cum siccatus est, tarde acerrimo; lamellis primo subalbis tum 311, umbrinis cum vulneratae sunt (301 t-4), inaequalibus, simplicibus, adnatis deinde subdecurrentibus, confertis; stipite albidulo (9 t-4 ad 311), viscidulo; sporis pallide luteis (36 t-2), late ellipticis, echinulatis, latis lineis reticulatis, 8.75–10.62 μ × 11.25–11.87 μ.

Type locality: Kelly Park, Rock Springs, Orange Co., Florida.

Habitat: In humus under mockernut or live oaks.

Distribution: The type locality and in woods near Lake Wildmere, Longwood, Florida.

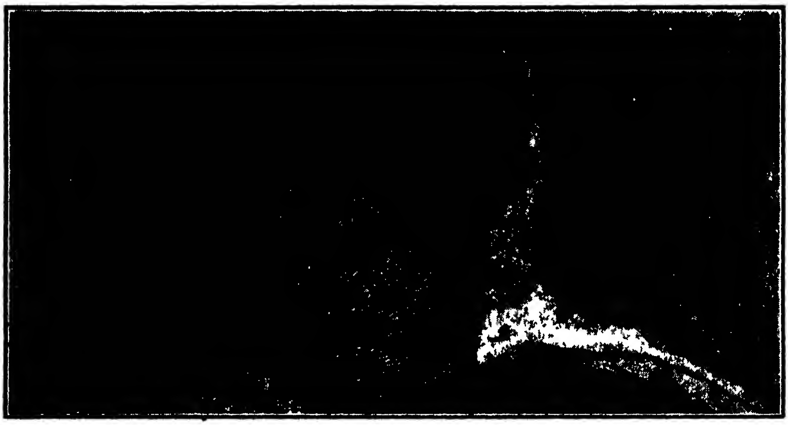


FIG. 4. *Lactaria fumeacolor* Burl. Natural size, type 2, Apr. 3–44.

This species was collected several times during November 1941, and twice in April 1944. Evidently it will normally occur at these times. Not having collected in these localities during summer, I cannot say whether the season for the species extends from April until November. From *Lactaria trivialis* Fries and *Lactaria limacina* Beards. & Burl. it differs in the latex staining the wounds raw umber and in the occasional zonate appearance. From the latter it also differs in the absence of agglutinated tangled tomentum on the margin of the pileus and in the maize colored spores. The latex is very abundant and when the cuticle is torn from the pileus, drops exude like beads of perspiration. The type collection is number 2 Apr. 3–1944, and part of it is deposited in the New York Botanical Garden, and part in my own herbarium.

Lactaria Beardslei sp. nov. (FIG. 5; 6, *E*)

Pileus broadly convex expanding to infundibuliform with margin sometimes becoming striate, up to 5.3 cm. straight across; surface brownish drab becoming raw umber to chocolate, pruinose to minutely floccose, zonate, with zones fading, viscid when wet; context in stipe raw umber, paler in the pileus, with an odor when broken fresh similar to that of *Lactaria camphorata* but not persisting, slowly peppery in young specimens; latex white unchanging, slowly a little peppery in the young stage; lamellae snuff brown tone 1 to dark fawn tone 1 singly, unequal, few forking, rounded at the outer end, narrower then rounded at the

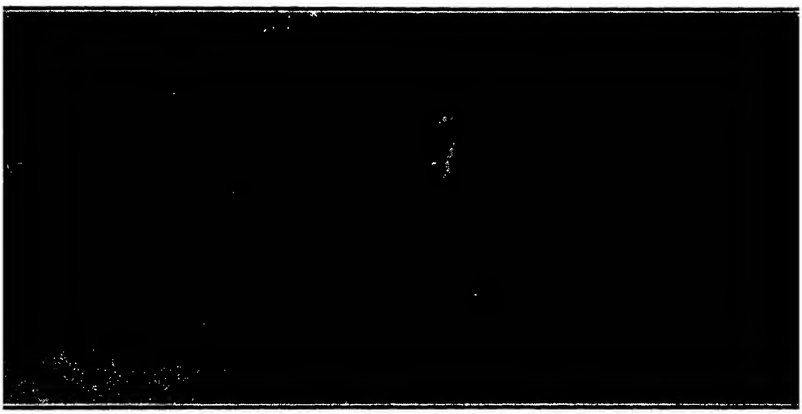


FIG. 5. *Lactaria Beardslei* Burl. Natural size, type 12, Dec. 29–43.

inner end, and attached by a decurrent tooth, rather broad, close; stipe mineral brown to brownish drab, pruinose, paler at the base and tomentose, equal to enlarged below, up to 5 cm. × 1 cm. at the apex to 1.5 cm. at the base or from 3 cm. × .8 cm.; spores fleshy-white, 7.5 × 8.1 μ to 8.1 × 9.37 μ, protuberances of unequal length and prominent under the 1/6 power, reticulate with connecting lines when stained with iodine and viewed under higher power.

Pileo late convexo, demum expanso et infundibuliformi, 2.3–5 cm. lato, brunneo (302, 343) aut umbrino (301), obscurioribus zonis notato, expallescenti, minute pruinoso-floccoso, viscido cum udus est; margine interdum striato; carne brunnea tincta, odore grato cum fracta est, simili odoris *Lactariae camphoratae*, sed absenti cum siccata est, tarde acri; lacte albo, tarde acri cum junior est; lamellis pallide brunneis ("Brun Havane" 303 t-1 ad 307 t-1), inaequalibus, paucis ad stipitem furcatis; stipite brunneo (339 ad 302), pruinoso .8–1 cm. × 3–5 cm.; sporis albidulis, 7.5–8.75 μ × 8–10 μ, echinulatis, reticulatis.

Type locality: Black Hammock, Oviedo, Florida.

Habitat: In rich soil rather open place in hammocks.

Distribution: Type locality and near Christmas, Florida.

This species differs from *Lactaria camphorata* (Bull.) Fries in the minutely pruinose-floccose surface which is viscid when wet, in the absence of odor in the dried state, and in the peppery taste in the fresh stage in the field, especially when young. From *Lactaria rimosella* Peck it differs in the surface being minutely pruinose-floccose rather than rimose, frequently zonate, and in the white latex. From *Lactaria helva* Fries it differs in the smaller size, frequently zonate appearance, viscidity when wet, more minute pruinose-floccose surface, lack of odor when dried, and in the habitually white latex. The color both fresh and dried is much darker. From *Lactaria mutabilis* Peck it differs in the pruinose-floccose surface of the pileus, its smaller size, the odor of the flesh, and the peppery taste of the latex in fresh young specimens.

Since the type and other collections were found in favorite collecting grounds of Prof. H. C. Beardslee, the specific name of this species seems very appropriate. Part of the type has been deposited in the New York Botanical Garden, and part remains in my herbarium.

Lactaria flocculosaceps sp. nov. (FIG. 6, *F*)

Pileus broadly convex, umbonate, then expanding and centrally depressed with arched margin which may become crenate and striate, 2.8–6.5 cm. broad; surface fulvous to mineral brown (333 t-1), azonate, minutely tomentose becoming flocculose and paler, dry; context with a weak odor similar to that of *Lactaria camphorata* or nearly exactly like that of slippery elm (*Ulmus fulva* Michx.) when freshly broken, and remaining for some time when dried; latex watery but not like whey, a little milky in very young specimens, mild; lamellae dark fawn (307) becoming fulvous, unequal, some forking near the stipe, adnate to decurrent, close; stipe colored like the pileus or slightly paler, pruinose to villose, becoming hollow, nearly equal, 1.7–4.5 cm. long by .4–.8 cm.; spores pale blush tone 3, echinulate without lines or bands, 6.87–7.5 $\mu \times$ 7.5–8.75 μ.

Pileo late convexo, umbonato, demum expanso et centro depresso, fulvo aut minerali-brunneo (339 t-1) azono, flocculoso, sicco, 2.8–6.5 cm. lato; margine arcuato, interdum crenato et striato; carne debili odore simili odoris

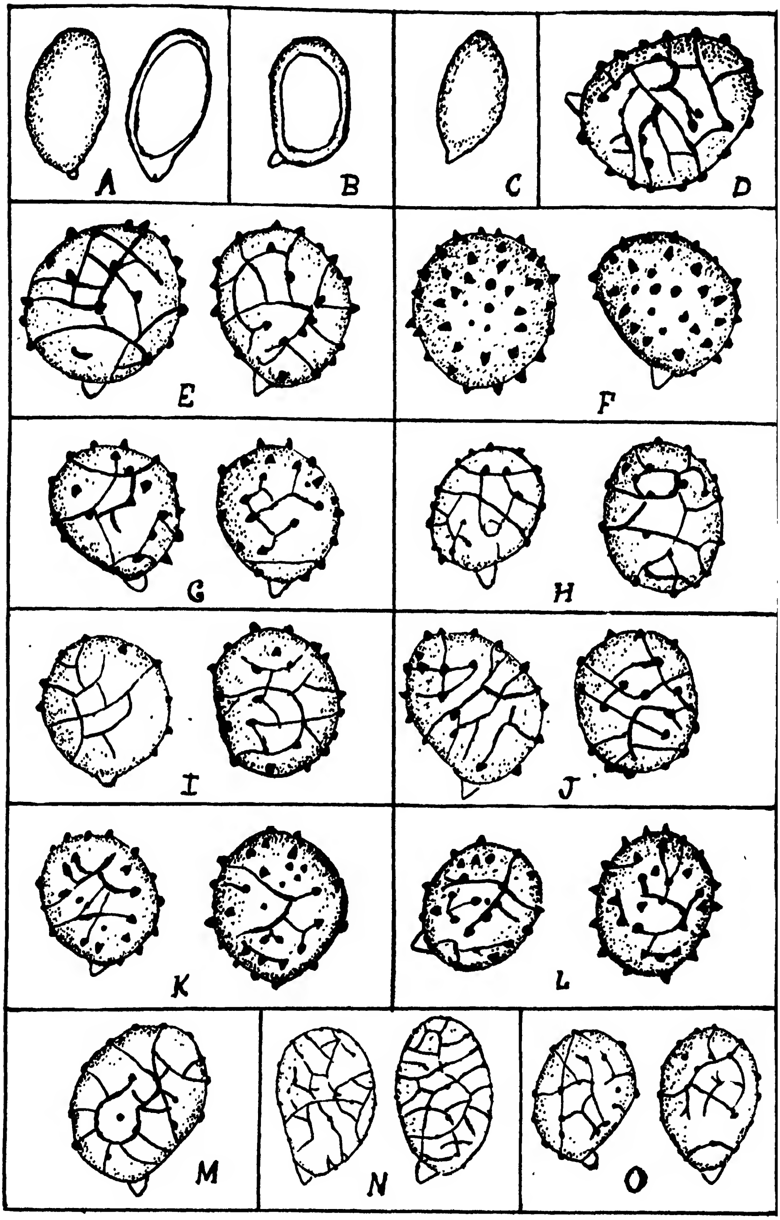


FIG. 6. Spores of *A*, *Lepiota cupressea; B*, *L. marginata; C*, *L. decorata; D*, *Lactaria fumeacolor; E*, *L. Beardslei; F*, *L. flocculosaceps; G*, *L. camphorata; H*, *L. helva; I*, *L. rimosella; J*, *L. mutabilis; K*, *L. alpina; L*, *L. isabellina; M*, *L. torminosa; N*, *L. floridana; O*, *L. villosa* Clem.

Lactariae camphoratae aut *Ulmi fulvae* Michx. cum fracta est et cum siccata est; lacte aqueo, aut interdum subalbo sed tenui cum junior est, miti; lamellis pileo pallidioribus (307), demum fulvis, inaequalibus, paucis ad stipitem furcatis, adnatis demum subdecurrentibus, confertis; stipite pileo concolore aut leviter pallidiore, pruinoso et villoso, demum cavo; sporis *echinulatis*, 6.87–7.5 μ × 7.5–8.75 μ.

Type locality: Kelly Park, Rock Springs, Orange Co., Florida.

Habitat: Rather open places in oak woods or mixed deciduous woods.

Distribution: The type locality, also near Apopka, Longwood and Oviedo, Florida, Cold Spring Harbor, Long Island, N. Y., near Boston, Mass., and Newfane Hill, Vermont.

This species resembles *Lactaria helva* Fries in color but differs in its smaller size, rarely becoming as large as the minimum size of the former, the more minute floccose covering of the pileus and in its spores which are coarsely echinulate without lines or bands. In Studies in the Agarics of Denmark, part VII, page 35, Dr. Lange mentions collections of *L. helvus* made in 1915 as having spores without "any trace of ribs." This might indicate either insufficient staining or magnification, or that *Lactaria flocculosaceps* may occur in Denmark. From *Lactaria rimosella* Peck with which it has undoubtedly been confused, it differs in the floccose covering of the pileus rather than a rimose-areolate surface, as well as in the spore pattern and the retention of the odor for some time after the mushrooms have been dried. The spore drawings of *Lactaria camphorata* and *Lactaria helva* have been made from specimens collected in Sweden, and those of *Lactaria rimosella* Peck from type specimens.

Lactaria alpina Peck is another small species with a tomentose-squamulose pileus but without odor and with an acrid white latex. From May 30 to the middle of August 1942, this species occurred abundantly at the edge of a cluster of white birches on Newfane Hill. The squamulose appearance develops as it matures. The spore drawings are from Peck's specimens in Albany, N. Y. (FIG. 6, *K*; FIG. 7).

In Quelques Champignons des Hauts-Marais Tourbeux du Jura by P. Konrad and J. Favre on page 153, *Lactaria isabellina* Burl. is given as a synonym of *Lactarius tabidus* Fries. From the description of this species as given by Fries *Lactaria isabellina*

differs in the cut or broken flesh and the drying latex becoming yellow, the crowded lamellae which are not flaccid and in not wasting away as the name *tabidus* implies. Fries in Monographia Hymenomycetum Sueciae **2**: 182. 1863, gives the taste of the latex as submild. The latex of *L. isabellina* is first *astringent* then acrid. The description of the species referred to *Lactarius tabidus* Fries by Konrad and Maublanc, cited by Konrad

FIG. 7. *Lactaria alpina* Peck.

and Favre, agrees fairly well with *Lactaria isabellina* Burl., and it is quite possible that it occurs in France and perhaps other parts of Europe. The question seems to be whether to interpolate in Fries' description characteristics which he did not include and disregard the *subdistant flaccid* lamellae, and the *wasting away* which seems to be the distinguishing feature of his species; or since Fries saw his species living and figured it, to accept his description as it stands and believe that there is a submembranaceous *Lactaria* with subdistant lamellae, white latex which is submild, not astringent, and which as a whole does *waste away* and for which the name "*tabidus*" with all it implies

would be appropriate. The spores of *Lactaria isabellina* are flesh color 67 tone 1 in mass and with iodine stain and oil immersion high power show some connecting lines between the protuberances (FIG. 6, *L*).

In North American Flora **9**: 178. 1910, I gave *Lactaria villosa* Clem. as a synonym of *Lactaria torminosa* (Schaeff.) Pers. Since critical examination of the spores had not been made, I have recently examined them according to Crawshay's method. While they resemble the spores of *L. torminosa* in shape and in general in the ornamentation, they average somewhat smaller. However, while the spores of *L. torminosa* were from a spore print made from a specimen collected in Sweden in 1930, the spores of *L. villosa* were taken from the lamellae of specimens distributed in 1896. Unless fresh living specimens could be examined I would not wish to regard the species as distinct from *L. torminosa*. It is plainly distinct from *Lactaria floridana* Burl. in having spores which are more broadly elliptical with larger and more numerous protuberances, and a much less reticulate pattern. It is also distinct in having long tomentum projecting from the edge of the pileus as in *L. torminosa*. (Drawings of the spores of the three species recently made with the same magnification and stain are shown in figure 6, *M*, *N*, *O*.) .

I wish to express my thanks to Dr. S. M. Zeller for specimens of *Lepiota decorata* Zell., and to Prof. Arthur T. Walker of the University of Kansas for editing the Latin descriptions.

WINTER PARK,
FLORIDA

NOTES ON FLORIDA FUNGI. III

ERDMAN WEST

(WITH 2 FIGURES)

ASCOBOLUS MAGNIFICUS Dodge.

This well-marked discomycete has been reported on horse dung from New York City and the West Indies. Typical specimens were collected on cow dung near Newman's Lake, Alachua County, on 10 September 1940. The greenish-yellow hymenium of immature specimens was in striking contrast to the brownish-black of nearly mature plants. The spore-sculpturing, a single longitudinal line, was well marked on many of the spores. There does not appear to be any previous record of the occurrence of this species in Florida (*F. 23686*).

DOTHICHLOE NIGRICANS (Speg.) Chardon.

This ascomycete has been collected several times in Florida during the past decade. The first collection made at Gainesville, Alachua County, 9 July 1931, was verified by W. W. Diehl. This was growing on upright stems of *Panicum hemitomon* Schult., a grass commonly called maiden cane (FIG. 1). Another collection made 27 July 1935 at Quincy in Gadsden County was on *Axonopus affinis* Chase, a pasture plant known as carpet grass. The infection is evidently systemic as all stems on the same plant are affected and show the stromata at the nodes. Flower or seed heads are not produced on infected plants (*F. 2961*, *F. 2962*, *F. 2965*.

PITHYA CUPRESSI (Batsch) Rehm.

Collected at Gainesville, Alachua County, 17 September 1941, by L. O. Gratz on foliage of *Cupressus* sp. This appears to be the first report of this fungus in Florida. The collection was made on a branch broken from a plant recently received from a Florida nursery. In view of this fact and the large numbers of *Cupressus* spp. and *Juniperus* spp. grown in Florida, the fungus

might be expected to be common here. That it has not been seen previously may be due in part at least to the relatively short duration of the delicate ascocarps in this warm, humid climate (*F. 24306*).

CINTRACTIA LIMITATA Clinton.

This is a rather inconspicuous smut that is reported as being common on *Cyperus ligularis* L. in Puerto Rico.[1] There appear to be no previous records of its occurrence anywhere else. The sedge is rather common near the coast in southern Florida but only once has it been found infected with the smut. A generous collection was made at Key West in Monroe County on 21 November 1930 (*F. 15397*).

CINTRACTIA MONTAGNEI (Tul.) Mag.

This inconspicuous smut was collected at Gainesville, Alachua County, on 17 June 1938 on the sedge *Rynchospora miliacea* (Lam.) A. Gray. This is a common species of sedge around flatwoods ponds but no other collections have been made on this previously unreported host. The identification of the smut was made by G. L. Zundel (*F. 20442*).

DOASSANSIA DEFORMANS Setch.

A collection on leaves of *Sagittaria lancifolia* L. in Orange Lake near McIntosh in Marion County was made on 2 July 1942. This fungus is not uncommon on this host in Florida but the conditions under which this particular infection occurred are rather interesting. The host is one of the dominant plants on the floating islands so common on this large, shallow, irregular lake. These islands, varying from three or four feet in diameter to thirty or forty feet, drift freely about the lake as they are blown by air currents. Their "soil" consists mostly of humus and decaying roots held together by the interlacing roots of the living vegetation. *D. deformans* has been noticed several times on *S. lancifolia* on these free-floating habitats (*F. 24399*).

[1] Sci. Survey of Puerto Rico and the Virgin Is. Vol. 8, part 1, p. 109. 1926.

FIG. 1 *Dothichloe nigricans* on *Panicum hemitomon*

SOROSPORIUM CONFUSUM H. S. Jackson.

Several species of the grass genus *Aristida* are very common but there are no reports of a smut on any of these in Florida. On 15 November 1941, Herman Kurz collected a specimen of *Aristida stricta* Michx. for dune-plant study and sent it to the author for determination. It exhibited more than three dozen sori of the smut, all confined to individual spikelets (*F. 23674*).

SOROSPORIUM SYNTHERISMAE (Peck) Farlow.

This widely distributed smut was collected on *Cenchrus* sp. in Manatee County by G. F. Weber, 10 November 1935, and on *C. pauciflorus* Benth. in Alachua County on 22 July 1941. Previously reported collections made in the Southeastern States include only North Carolina and Mississippi so that this is the first record from Florida (*F. 21259*, *F. 23689*).

TESTICULARIA CYPERI Klotzsch.

The existing reports of the occurrence of this conspicuous smut are few despite the fact that the original description was published over a century ago. In one northern state, New York, it was parasitizing *Rynchospora macrostachya* Torr.; in the three southern states, Texas, Louisiana and Florida, it has been reported on *R. corniculata* (Lam.) A. Gray, a very closely related species. Edgerton and Tims [2] indicated that the fungus was not uncommon in Louisiana. In Florida, collections have been made at a number of widely separated points since it was first collected by the late Severin Rapp in Seminole County in 1921 as reported in Lloyd's Notes.[3]

Collections are on file from the following counties in Florida: Alachua, Clay, Dixie, Levy, Putnam, Orange, and St. Johns. A careful search would very probably prove that the range of the smut is coextensive with that of the host, at least in Florida.

Illustrations and reports so far published tend to indicate that very few sori are produced on a single host plant. This is not true in Florida as several stems have been found each bearing over 100 sori (FIG. 2) and stems carrying 10 to 20 sori are not at all uncommon (*F. 7473*, *F. 22706*, *F. 21344*, *F. 21343*, *F. 23688*, *F. 7472*, *F. 30035*).

[2] Edgerton, C. W. and Tims, E. C. Mycologia 18: 169–170. 1926.

[3] Lloyd, C. G. Myc. Notes 7: 1130. 1922.

FIG 2 *Testicularia Cyperi* on *Rynchospora corniculata*

USTILAGO SPHAEROGENA Burrill.

Collected on *Echinochloa crus-galli* (L.) Beauv. in the Everglades by H. H. Wedgeworth at Belle Glade, Palm Beach County, on 3 July 1931. This fairly generous collection was determined by G. L. Zundel. A very sparse collection was made on the same host along Newnan's Lake near Gainesville, Alachua County, on 30 July 1931. There are no previous reports of its occurrence in Florida (*F. 7461*, *F. 7462*).

USTILAGO TENUISPORA Ciferri.

The common smut, parasitizing the panicles of various species of *Polygonum* in Florida, has been considered to be *Ustilago utriculosa* (Nees) Tul. However a collection made 8 September 1940 in Alachua County on *Polygonum punctatum* Ell. was identified by G. L. Zundel as *Ustilago tenuispora* Ciferri. This constitutes the first record of the finding of this species in North America, all previous records being from the southern hemisphere. *U. tenuispora* differs from *U. utriculosa* chiefly in having spores only 6–8 μ in diameter instead of 9–14 μ. Study of older collections in the herbarium has revealed the fact that this species was collected in Alachua County as early as March, 1927, but not distinguished from *U. utriculosa*. Other collections indicate its wide distribution in this county, while its occurrence in other areas is proved by a collection made 20 May 1941 near Cook's Hammock in Lafayette County. All of the collections have been on the same host (*F. 23762*, *F. 23754*, *F. 7401*).

AECIDIUM CYRILLAE Arthur.

The geographic range of this fungus was recently [4] extended to include two counties in Florida. While examining several large colonies of *Cyrilla parvifolia* Raf. in Cook's Hammock in Lafayette County on 20 May 1941, numerous heavily infected plants were discovered. The infection was so severe on many individuals of this new host that only an occasional leaf was found free from pycnia or aecia. A few of the green twigs were found bearing aecia indicating that the fungus is occasionally caulicolous (*F. 32560*, *F. 32561*).

[4] West, E. Mycologia **33**: 40. 1941.

COLEOSPORIUM IPOMOEAE (Schw.) Burrill.

The uredia and telia of this rust are common in Florida on many species of wild morning glories. Two collections have been made on an introduced species, *Ipomoea cairica* (L.) Sweet, the first at Ruskin in Hillsborough County, 7 November 1935, by G. F. Weber and another near Vero Beach in Indian River County, 8 November 1940, by R. K. Voorhees. There appear to be no previous reports on this host in the United States. A collection made by G. F. Weber on *Ipomoea setosa* Ker. on 3 October 1923 at Gainesville in Alachua County is apparently the same species of rust (*F. 16666*, *F. 22641*, *F. 4969*).

COLEOSPORIUM LACINIARIAE Arthur.

This common rust attacks many species of *Laciniaria* in Florida. One of the largest and most conspicuous species, *L. scariosa* (L.) Hill, has not been found infected until recently, even where it was closely associated with heavily infected individuals of *L. elegans* (Walt.) Kze. and *L. laxa* (Pursh.) Kze. On 15 September 1940 several plants were found in Alachua County bearing scattered sori on both large basal and smaller upper leaves in a dry oak woods in the vicinity of longleaf pine (*F. 22657*).

COLEOSPORIUM TEREBINTHINACEAE (Schw.) Arthur.

This rust was collected inadvertently on 7 October 1940 by W. A. Murrill near Monticello in Jefferson County while obtaining specimens of *Silphium Simpsonii* Greene for the phanerogamic herbarium. This rust has not been previously reported on this host nor in Florida (*F. 23676*).

GYMNOSPORANGIUM ELLISII (Berk.) Farl.

The witches brooms caused by this rust have been observed in western Florida for many years but no colonies of the telial host, *Chamaecyparis thyoides* (L.) B.S.P., were known to occur naturally east of the Ocklocknee River until a forestry student turned up one in Putnam County nearly 200 miles farther east. A visit made to this area resulted in finding an abundance of waxmyrtle (*Myrica cerifera* L.) severely diseased and bearing great numbers of aecia on leaves and stems. This collection

was made 29 May 1942 near Interlachen in Putnam County (*F. 24396*).

GYMNOSPORANGIUM TRANSFORMANS (Ellis) Kern.

This rust was known only from a small group of northeastern states until reported from Florida [5] in 1939. While visiting the group of *Chamaecyparis* in an eastern Florida county mentioned in a preceding note, the aecial stage was found on almost every specimen of *Aronia arbutifolia* (L.) Ell. that was present in the area. The shrub was not abundant but the individuals were badly diseased and in many cases severely deformed. The collection was made 29 May 1942 near Interlachen, Putnam County (*F. 24395*).

PUCCINIA CENCHRI D. & H.

The common rust of sandspurs is widely distributed and common in Florida on the tall sandspur, *Cenchrus echinatus* L., and has been collected occasionally on *C. pauciflorus* Benth., a host previously reported only from Oklahoma. The most robust sandspur, the coastal species, *Cenchrus tribuloides* L., has not been reported as a host of this fungus. On 27 August 1943 at Lake Worth in Palm Beach County, a colony of *C. tribuloides* on the ocean side of the dunes was found to be generally infected and a collection was obtained (*F. 23268*, *F. 32301*).

PUCCINIA EVADENS Hark.

The uredinial stage has been collected once on *Baccharis angustifolia* Michx. in Dade County, 3 September 1942. This seems to be the first record of a rust on this host although other species of *Baccharis* are commonly affected (*F. 21303*).

PUCCINIA FUIRENAE Cooke.

The rust on *Fuirena* has been reported on all three species of the *squarrosa* group as follows: on *F. breviseta* Cov. in Florida; on *F. hispida* Ell. in Alabama; and on *F. squarrosa* Michx. in South Carolina. The rust was recently collected again in Alachua County on *F. breviseta*. An examination of two collections in the herbarium revealed that the host was *F. hispida* Ell.,

[5] West, E. Mycologia 31: 425. 1939.

and not *F. squarrosa* Michx. as indicated on the label. These collections were made at Lake City, Columbia County, on 7 August 1900 by H. H. Hume and 17 November 1900 by Lucia McCulloch (*F. 5361*, *F. 5362*).

PUCCINIA HYPTIDIS-MUTABILIS Mayor.

A common bushmint, *Hyptis mutabilis* (A. Rich.) Briq., is widely distributed in Florida and usually shows evidence of infection with a rust fungus. With the exception of pycnia, any stage or all three may be present on almost any individual of this species that is examined during the growing season. For many years this rust has been labeled *Puccinia Hyptidis* (Curt.) Tracy & Earle probably because no careful examination was made of the teliospores. These are, in all cases examined so far, definitely thickened at the apex and in most other characters correspond to those of *P. Hyptidis-mutabilis* Mayor. Collections have been in Alachua, Columbia, and Gadsden Counties. The rust on a related plant, *H. radiata* Willd. in Florida, appears to be good *P. Hyptidis* (*F. 5119*, *F. 16819*, *F. 24583*).

PUCCINIA LEONOTIDICOLA P. Henn.

The weed commonly called lion's tail (*Leonotis nepetaefolia* R. Br.) is widely distributed in Florida but despite many years of searching has never been found infected with a rust. On 8 November 1943 Arthur S. Rhoads and Phares Decker found infected leaves on nearly every plant growing in an abandoned sand-pear orchard near Ocala, Marion County. Only the uredinial stage was found in this case. The rust has been reported from the West Indies and South America but there are no previous reports from the mainland of the United States. The identification was made by Dr. George B. Cummins (*F. 7585*).

PUCCINIA LEVIS (Sacc. & Bizz.) Magn.

An introduced plant commonly called Natal grass (*Tricholaena repens* (Willd.) Hitchc.) is widely distributed in Florida especially from Gainesville southward. It has been remarkably free from fungous diseases although *Cerebella Andropogonis* Ces. is occasionally found in the seed heads. Several times during the summer of 1942, the writer found uredia of a rust on the lower

leaves of one vigorous clump. Finally on 19 August 1942, a generous collection of this stage was made but only a very few teliospores could be found.

In 1925, Fragoso and Ciferri[6] described *Uromyces Tricholaenae* on this host from Santo Domingo and described one-celled teliospores. However, Kern[7] after examining part of the type material was inclined to believe that the Santo Domingo rust was *P. levis*.

Part of the Florida collection was submitted to G. B. Cummins who considered it *Puccinia levis* despite the paucity of teliospores. This collection represents the first record of this rust on this host on the mainland of North America. Another collection made 5 January 1943 from the same clump of grass provided a generous quantity of teliospores, corresponding to those of *P. levis* in all respects except size. Over fifty per cent in the mounts counted measured 40–44 μ in length (*F. 28054*, *F. 24584*).

PUCCINIA OBLIQUA Berk. & Curt.

This short cycle species has been reported from the southeastern states on several members of the Asclepidaceae. In Florida it is especially common on *Seuteria palustris* (Pursh.) Vail along the seacoast. It has not been reported on *Metastelma scoparium* Nutt. but was collected on that host at Gainesville in Alachua County on 25 May 1933 and again at Key West in Monroe County on 3 November 1934 (*F. 6065*, *F. 16356*).

PUCCINIA PODOPHYLLI Schw.

The host (*Podophyllum peltatum* L.) of this rust occurs sparingly in a very few counties along the northern boundary of Florida but there is no report of the rust in this state. A generous collection of the aecial stage was made in a hammock along the Chipola River north of Marianna in Jackson County, 16 March 1937 (*F. 16370*).

PUCCINIA VIOLAE (Schum.) DC.

The rust of wild violets is widely distributed on many species of violets in the United States. It has never been found abun-

[6] Fragoso and Ciferri. Bol. R. Soc. Esp. Hist. Nat. **25**: 357 (1925).
[7] Kern, F. Mycologia **20**: 79. 1928.

dantly in Florida and is reported on only one species, *V. primulifolia* L., in Arthur's Manual of the Rusts. Two previously unreported hosts have been found in the vicinity of Gainesville, Alachua County. Telia were collected on *V. Walteri* House in Sanchez Hammock on 9 April 1935 and on *V. floridana* Brainerd in Sugarfoot Hammock on 13 March 1940 (0, I) and 26 June 1940 (II, III) (*F. 6585*, *F. 17012*).

UREDO CEPHALANTHI Arthur.

This rust is reported from southern Florida and Cuba. Additional Florida collections have been made in Alachua and Levy counties in the northern part of the peninsula, indicating that the range of the fungus is probably much wider than previously reported. The disease is not conspicuous on the upper surface of the leaves even when the uredia are abundant on the lower side (*F. 4365*, *F. 21367*, *F. 22331*).

UREDO LAETICOLOR Arthur.

This rust is recorded from the West Indies on *Ipomoea dissecta* Jacq. Several collections have been made in Florida on this same host which is widely planted as an ornamental and has become naturalized in several localities. Collections are on file from Polk County by G. F. Weber on 17 November 1923, Alachua County by the same collector on 3 November 1923, and Polk County by W. B. Tisdale on 18 June 1932. It is not uncommon in the vicinity of Gainesville, but has not been hitherto reported from Florida (*F. 4370*, *F. 4371*, *F. 17117*).

UREDO SAPOTAE Arthur & Johnston.

At the Subtropical Experiment Station, Homestead, Dade County, George D. Ruehle collected a rust on the leaves of seedling sapodilla trees (*Achras zapota* L.) in January 1942. This proved to be *Uredo Sapotae* Arthur & Johnston, a species hitherto reported only from the West Indies. This finding was recorded in the Plant Disease Reporter [8] (*F. 23678*).

UROMYCES COMMELINAE (Speg.) Cooke.

This rust is not uncommon in Florida on *Commelina angustifolia* Michx., an inhabitant of dry sandy regions, but it has not

[8] Ruehle, G. D. Plant Disease Reporter 26: 261–2. 1942

been reported on any other species. On 12 August 1942 the fungus was found infecting the leaves and stems of *C. elegans* H.B.K., a typical hammock plant, on the Campus of the University of Florida at Gainesville, Alachua County. Collections made at Cocoa in Brevard County by A. S. Rhoads on 30 June 1933 and again on 19 December 1936 appear to be on the same host. It has been previously reported on *C. elegans* only in the West Indies (*F. 23392*, *F. 24597*, *F. 16742*).

UROMYCES SPERMACOCES (Schw.) Curt.

The uredia are frequently collected in Florida on *Diodia teres* Walt., the only host reported in Arthur's Manual of the Rusts. A related plant, *Diodia tetragona* Walt., a creeping plant in moist situations, is common in many parts of Florida. *U. spermacoces* was collected on this plant 29 May 1937 near Lawtey in Bradford County, near Raiford in Union County on 22 May 1942, and in Flagler County on 25 June 1942. In contrast to the normal creeping habit of this new host, infected branches are stiffly erect and bear ascending leaves so that diseased individuals are easily distinguished in colonies of healthy plants (*F. 16804*, *F. 24397*, *F. 24401*).

Cercospora Forestierae West, sp. nov.

Maculae suborbiculares vel irregulares, 3–10 mm. in diametro, saepe confluentae, rubro-brunneae; stromatis tuberculatis, hypophyllis vel amphigenis; conidiophoris fasciculatis, brunneis, tortuosis, 1–3 geniculatis, 3–6 × 60–120 μ; conidiis distincte obclavatis, ad bases fulvo-brunneis, ad apices hyalinis, pleuriseptatis, 2.5 × 5–6 × 85–110 μ.

While on a foray along the Suwannee River near Hart Springs in Gilchrist County on 1 October 1943, the common forestiera (*Forestiera acuminata* (Michx.) Poir.) was noticed to be severely diseased by a *Cercospora* leaf spot. No record was found in the literature of any species of *Cercospora* on this host. Furthermore no species of *Cercospora* reported on other members of the Oleaceae could be matched with this one on forestiera. It is therefore considered worthy of designation as a new species.

The spots are irregularly circular in shape, marginal, apical or more or less central, tawny to Dresden brown,[9] 3–10 mm. or

[9] Ridgway, R. Color Standards and Nomenclature, 1912.

more in diameter, coalescing to include half or more of the area of some leaves.

Mycelium internal; stroma tuberculate, hypophyllus or amphigenous; conidiophores fasciculate, dark fuscous, tortuous, 1–3-geniculate, scars prominent, 80–120 μ high, 3.5–6 μ in diameter. Conidia mostly 85–110 μ long, some shorter, 5–6 μ thick near base, 2.5 μ towards tips, fuscous at base fading to hyaline at the tip, obclavate, rather abruptly and conspicuously enlarged below (4 or 5 cells), 7 to 11 septate (*F. 2652*).

SEPTORIA PACHYSANDRAE Dearness.

On 15 March 1937, a severe leaf-spotting disease of Allegheny pachysandra (*Pachysandra procumbens* Michx.) was noted in a small area of a natural stand in a hammock along the Chipola River near Marianna in Jackson County. Examination in the laboratory proved the organism associated with the spots to be a species of *Septoria*, apparently unnamed and it was so labeled. More recently this fungus has been described [10] as a new species by John Dearness from collections made in Tennessee. The Florida collection extends the range of the fungus to the southern limits of its host range (*F. 24605*).

SIROSPHAERA CHLOROSTOMA Petch.

Three collections of this fungus growing and fruiting on various species of entomogenous fungi have been made in Florida. The first occurred at New Port Ritchey in Pasco County on 15 March 1932 where the host was cinnamon fungus, *Verticillium cinnamoneum* Petch. A second collection was obtained at Mandarin in Duval County on 13 December 1933. In this case the host was obscured by the *Sirosphaera* but appears to be a species of *Aschersonia*. The third collection originated near Gainesville in Alachua County on 10 October 1939. The host is *Aegerita Webberii* Fawcett which has been mentioned by Petch [11] as a host for this fungus in Ceylon and Florida. There does not seem to be any record of its occurrence on *Verticillium* or *Aschersonia* (*F. 10799*, *F. 10477*, *F. 22210*).

[10] Mycologia 33: 362. 1941.
[11] Petch, T. Trans. Brit. Myc. Soc. 11: 65–66. 1926.

Sirosperma floridana West, sp. nov.

Pycnidiis globosis, nigris, 90–110 μ diametro, in subiculo nigro formatis; parietibus pseudoparenchymatis, ostiolo nullo; conidiis hyalinis, ellipsoideis, 3.5 × 1.8–2.4 μ.

Collected at Homestead in Dade County on 16 May 1933 (Type) on *Aschersonia* sp. on whiteflies on grapefruit leaves; on 8 February 1941 in the same locality on the same hosts.

During the past 10 years, a black fungus apparently parasitic on the entomogenous fungus *Aschersonia* has been collected twice on grapefruit leaves. The conspicuous olive-black patches 5–10 mm. in diameter are centered on the immature stromata of the *Aschersonia*, thinning out to an indeterminate margin as they spread over the adjacent leaf surface. When thoroughly dried, the whole patch including the *Aschersonia* and parasitized white-fly is easily detached from the leaf. Adjacent colonies coalesce and in some cases half a leaf is covered by the black fungous growth.

Near the center of the patch, minute black pycnidia are borne in great profusion but these gradually decrease in numbers toward the margin. These pycnidia are entirely superficial, seated upon a subiculum not borne in or on a stroma, nor is there any tendency for the pycnidia to coalesce. The wall of the pycnidium is thin, composed of pseudoparenchymatous cells, two layers at the top, three from about the middle to the base. The walls of the cells are dark brownish-black with no greenish color evident under the microscope.

The pycnidia are filled with hyaline one-celled spores which do not separate easily in water and are arranged in a more or less columnar manner. Their origin is not apparent for no conidiophores have been observed.

These characters fit well into the genus *Sirosperma* of Sydow of which two species have been described, both occurring on entomogenous fungi. *S. Hypocrellae* Syd., the type of the genus collected in New Guinea on *Hypocrella* sp., has spores measuring 2–3 × 1.5 μ. *S. sparsum* Petch, collected in England on *Cephalosporium* sp., has spores 1.5–2 × 1 μ. The spores of the Florida fungus measure 3.5 × 1.8–2.4 μ.

Considering the significant deviation in spore size of the Florida fungus from those previously described, it seems desirable to consider it a new species (*F. 10478* Type, *F. 23128*).

Sphacelia Tricholaenae West, sp. nov.

Carnosa, obconica vel obovoidea, albida vel cremea, circa 1 mm. alta, ex ovario graminis oriunda; sporophoris anguste clavulatis, hyalinis, dense fasciculatis, 1.2–2 μ latis; conidiis singulatim acrogenis, oblongis, hyalinis, 12–15.5 $\times$ 5–6 μ.

Hab. in floribus tricholaenae repentis.

During the late summer and fall of 1942, several patches of Natal grass (*Tricholaena repens* (Willd.) Hitchc.) in the vicinity of Gainesville were examined periodically for the presence of parasitic fungi, especially rusts, smuts and ergot. On 10 November 1942, several inflorescences were found bearing the conidial stage of a fungus, apparently *Claviceps* sp. In some panicles, more than fifty per cent of the flowers were infected but a hand lens was necessary to detect their presence because of the small size of the fungous growth and the copious hairs on the floral parts of the host. This collection was recently reported as *Sphacelia* sp.[12]

The fungous body is fleshy, obconic to obovoid, white to creamy in color. The distal portion spreads the floral parts of the grass slightly but does not extend beyond them. The conidiophores are narrowly clavate, about 1.2–2 μ wide and densely crowded together. The viscous mass of spores clings among the copious hairs on the glumes. The conidia are oblong or short cylindrical, smooth, hyaline, 12–15.5 $\times$ 5–6 μ (*F. 32962* type).

FLORIDA AGRICULTURAL EXPERIMENT STATION,
GAINESVILLE, FLORIDA

[12] West, E. Plant Disease Reporter **27**: 113–4. 1943.

THE GENUS LAMPRODERMA AND ITS RELATIONSHIPS. I[1]

Mary Louise Dennison

(with 22 figures)

This study of the genus *Lamproderma* was undertaken in an attempt to clarify its taxonomic position with reference to related genera in the Lamprodermaceae as well as in the Stemonitaceae, and to formulate a clearer conception of the boundaries of the genus itself and of its species. *Lamproderma* is one of many myxomycete genera whose position has often been shifted. It is also representative of those genera in which there have been many species described from time to time without adequate basis, hence many specific names have been proposed which have come to be recognized as synonyms. Meylan has described numerous species belonging to this genus. Some of them seem to be valid, some were proposed on what seems to be inadequate material and still others may be interpreted as responses to environmental conditions at the time of fruiting.

In the Myxomycetes the category *variety* has been extensively employed. It has, however, been used by so many authors to mean so many different things that it has very little value so far as this group is concerned. It has been applied to designate differences which appear to be due merely to environmental influences which, in some cases, may be associated with fluctuations in local climate, in others, with fundamental climatic difference, such as that between lowland and alpine habitats or between temperate and tropical environments. As a result, the term is highly ambiguous and might well be discarded.

The category *subspecies*, to indicate more or less constant variations which occur fairly frequently and in various localities, might well be applied to some of the forms now known as varie-

[1] This work was done in the mycological laboratory of the State University of Iowa under the direction of Professor G. W. Martin.

ties, while those differences which seem clearly to be responses to environmental influences should, if it seems necessary to designate them by names, be called *forms*. In many cases any name would seem to be superfluous and the specific description should merely be broadened to incorporate such variant fruitings.

In the treatment to follow, certain varieties described by other authors are listed as such only because of lack of material for study. In most instances it is believed that they represent fruiting responses or minor variations which merge into the typical expression of the species with which they are associated.

The study was based on the material in the herbarium of the State University of Iowa, which includes the Morgan and Wingate collections as well as numerous specimens gathered and determined by Berkeley, Bethel, Bilgram, Ellis, Farlow, F. A. Gilbert, H. C. Gilbert, Hagelstein, Harvey, Macbride, Martin, Plunkett, Rex and Shimek in North America and Brandza, Jaap, A. and G. Lister, Meylan and Sydow in Europe.

Of the thirteen species of *Lamproderma* here regarded as valid, material of seven, one of which represented part of the type collection, had been collected and determined by the authors of the species. Types or authentic specimens of several of the species here relegated to synonymy or regarded as doubtful, were also studied.

Each specimen examined was studied first macroscopically by means of a binocular microscope, then microscopic mounts were made by wetting with 95 per cent alcohol, replacing this with a 3 per cent solution of potassium hydroxide, which restores the shape and size of the spores and other structures, and examining microscopically under low power, high dry and oil immersion objectives.

Hagelstein believes that potassium hydroxide "has a tendency to alter the color of spores of certain species." In the case of *Trichia* and related genera this is often strikingly true but in *Lamproderma* and its relatives this was not apparent except in the case of mounts allowed to stand in the KOH for several days, after which time both spores and capillitium frequently became pale. The use of freshly prepared mounts in KOH was found to be more satisfactory than that of water mounts. No dis-

coloration of spores or capillitium was observed when they were studied immediately.

In order to preserve specimens of which there was little material, permanent mounts were made in glycerine and sealed with balsam.

In the following pages the attempt is made to use certain terms consistently in describing spore markings. In order to eliminate possible confusion or misunderstanding, the specific meaning of each term, as based on Ainsworth and Bisby, "A Dictionary of the Fungi," 1943, and applied in this treatment, will be defined: punctate—marked with very small points, spots or hollows; verrucose—covered with small rounded processes or warts; echinulate—studded with small pointed processes or spines; aculeate—having long narrow spines.

The genus *Lamproderma* was proposed by Rostafinski in 1873 (Versuch 7) for species which had previously been referred to *Physarum* or *Stemonitis*. Rostafinski circumscribed his new genus adequately and placed it in what he called the tribe Stemonitaceae, with which it has been more or less associated ever since. Inasmuch as *Lamproderma* exhibits characters which indicate relationship with several other genera a short resume of the taxonomic treatment of the genus up to the present follows.

In the Versuch, the Ordo Amaurochaetae included five tribes, now regarded as families, namely, the Stemonitaceae, including the genera *Stemonitis*, *Comatricha* and *Lamproderma*, and the four monogeneric families Amaurochaetae, Echinosteliaceae, Enerthenemaceae and Brefeldiaceae. In 1874–75 Rostafinski published his monograph, followed by a supplement in 1876, but in neither of them was there any essential change made in his previous classification.

Massee, in his monograph (1892), divided the order Columelliferae into two sub-sections, or families as they are now regarded, the Stemonitae which embraced the genera *Stemonitis*, *Amaurochaete*, *Brefeldia*, *Reticularia*, *Siphoptychium* (*Tubifera*) and *Rostafinskia* (*Comatricha* in part), and the Lamprodermeae composed of *Enerthenema*, *Lamproderma*, *Echinostelium*, *Raciborskia* (*Comatricha* in part), *Orthotricha* (*Clastoderma*) and

Ancyrophorus (*Enerthenema*). The sub-sections were distinguished on the basis of the origin of the capillitium, this originating from every part of an elongated columella in the Stemonitae, and mainly from the apical portion of a short or elongated columella in the Lamprodermae.

Morgan (1894) distinguished the Stemonitaceae "by the brown persistent capillitium, arising from a lengthened columella, and rigidly maintaining the form of the sporangium." The genera included are *Clastoderma*, *Lamproderma*, *Comatricha*, *Stemonitis*, *Enerthenema* and *Diachea*. Of *Diachea*, Morgan states, "this genus is scarcely to be distinguished from *Lamproderma*, except by the white mass of lime which fills the tube of the stipe and columella."

Lister (1894) defined the Stemonitaceae as having stipitate sporangia with a delicate membrane, often evanescent; the stalk extending into the sporangium as a columella, from which the branching threads of the capillitium take origin. The following five genera were included: *Stemonitis*, *Comatricha*, *Enerthenema*, *Lamproderma* and *Clastoderma*. *Echinostelium* and *Raciborskia* are listed as allied genera; the latter with the suggestion that it applies to *Comatricha obtusata*. The order Amaurochaetaceae embraced the genera *Amaurochaete* and *Brefeldia* and was separated from the Stemonitaceae on the basis of the aethalial type of fruiting body.

Macbride (1899) divided the Stemonitaceae into three families, (1) the monogeneric Amaurochaeteae, (2) the Stemoniteae, which embraced the genera *Brefeldia*, *Stemonitis*, *Comatricha* and *Diachea*, and (3) the Lamprodermeae, which included *Enerthenema*, *Clastoderma* and *Lamproderma*.

Lister (1911) added the genus *Echinostelium* to the Stemonitaceae; Macbride (1922) added *Echinostelium* to the Lamprodermeae.

In the treatment of the Stemonitaceae in the third edition of the Lister Monograph (1925), the family is so defined as to include the genera *Barbeyella*, *Clastoderma*, *Comatricha*, *Echinostelium*, *Enerthenema*, *Lamproderma* and *Stemonitis*. Macbride and Martin (1934) include in the Stemonitaceae the genera

Amaurochaete, *Brefeldia*, *Comatricha*, *Diachea*, *Schenella* and *Stemonitis*. They recognize the family Lamprodermaceae as including those forms having a rather persistent peridium and capillitial branches arising from the apex of the columella, and embracing the genera *Barbeyella*, *Clastoderma*, *Diacheopsis*, *Echinostelium*, *Enerthenema* and *Lamproderma*.

In the Lister Monograph, *Amaurochaete* and *Brefeldia* are placed in a separate family, the Amaurochaetaceae. *Diachea* is placed in the Physaraceae because the capillitium and columella possess non-crystalline lime. *Schenella* was described in 1911 by Macbride, but was not treated in the 1922 edition of "N. A. Slime-Moulds," nor was it discussed by Lister in 1925. In Macbride and Martin this genus is placed in the Stemonitaceae. Its position is doubtful, but on the basis of its dark spores and abundant dark capillitium it may be accommodated in that family, at least temporarily. *Diacheopsis* was well described by Meylan (1930). On the basis of its membranous peridium with metallic lustre, its anastomosing capillitial filaments and its blackish purple spores, there appears to be little doubt of its affinity with *Lamproderma*.

Hagelstein (1944) follows Lister's treatment of the Stemonitaceae very closely. He includes *Clastoderma*, *Comatricha*, *Echinostelium*, *Enerthenema*, *Lamproderma* and *Macbrideola* in the family. *Barbeyella* is not treated since it has not been reported from North America. *Amaurochaete*, *Brefeldia* and *Schenella*, the latter with considerable reservation, comprise the Amaurochaetaceae. The genus *Diachea* in Hagelstein is referred to the Physaraceae in accordance with the precedent established by Lister.

It is here proposed to discard the family Lamprodermaceae of Macbride and Martin and to enlarge the Stemonitaceae so as to embrace all genera except *Echinostelium* included in the two families by Macbride and Martin, and to add to this enlarged family *Macbrideola* and *Elaeomyxa*.

Echinostelium, with its pale spores, its sparse and loosely arranged, spinose capillitium and its early loss of a peridium, should be removed from the Lamprodermaceae and placed in a

family of its own, the Echinosteliaceae, thus reviving a family established by Rostafinski in 1873. Macbride and Martin state, "*Echinostelium* may or may not belong in this family [Lamprodermaceae], but may at least be temporarily accommodated."

Hagelstein regards his new genus *Elaeomyxa* as justifying the establishment of a new family, the Elaeomyxaceae. The presence of a waxy substance in the fructification does not constitute any better reason for placing it in a family of its own when the other characters indicate relationship with the Stemonitaceae, as defined above, than the presence of lime with the combination of similar characters justifies the erection of a special family for *Diachea*. I propose therefore to incorporate this genus in the Stemonitaceae on the basis of its membranous sporangial wall, its capillitium of anastomosing and branching purplish threads, and its close resemblance to *Diachea*.

The justification for placing *Macbrideola* in the Stemonitaceae may appear a little remote. Because of its poorly developed capillitium, it suggests *Echinostelium*, which has just been removed from the family, but it has little else in common with that genus. Its undivided columella, resembling that of *Enerthenema*, its fairly persistent membranous peridium and its dark spores are evidence favoring its inclusion in the Stemonitaceae.

The Stemonitaceae as here discussed will, then, include the following genera: *Amaurochaete*, *Barbeyella*, *Brefeldia*, *Clastoderma*, *Comatricha*, *Diachea*, *Diacheopsis*, *Elaeomyxa*, *Enerthenema*, *Lamproderma*, *Macbrideola*, *Schenella*, and *Stemonitis*.

LAMPRODERMA Rost. Versuch 7. 1873.

Fructification sporangiate, stipitate or sessile, globose or ellipsoidal; peridium tough, membranous, persistent, shining with metallic iridescence; columella cylindrical or clavate, ⅓ to ⅔ the height of the sporangial cavity, rarely lacking; capillitium arising mainly from the apex of the columella, branching and anastomosing freely, the branches becoming more numerous and thinner as they approach the periphery; spores dark in mass.

Type: *Physarum columbinum* Pers.

KEY TO SPECIES OF LAMPRODERMA

a. Spores reticulate over all or a portion of the surface; sporangia sessile or short stalked . . . . b

a. Spores not reticulate, nearly smooth, punctate, verrucose, echinulate or aculeate; sporangia sessile to long stalked . . . . d

b. Spores regularly reticulate with raised bands which form a border 1. *L. cribrarioides*

b. Spore reticulation various, of warts or crests c

c. Spores marked with large, vesicularly warted crests; capillitium pale to purplish . . . . 2. *L. cristatum*

c. Spores strongly verrucose, the warts frequently arranged in lines over a portion of the spore; capillitium dark, attached to the peridium by small enlargements of the tips of the filaments . . . . 3. *L. robustum*

d. Peridium silvery-blue, dotted with black, depressed spots 4. *L. Gulielmae*

d. Peridium iridescent, not dotted with black depressed spots . . . . e

e. Sessile; columella lacking; sporangiate or sometimes plasmodiocarpous . . . f

e. Stalked or rarely sessile (*L. Carestiae*); columella present; sporangiate . . . g

f. Spores dark brownish purple, closely echinulate, 18–19 μ 5. *L. insessum*

f. Spores blackish purple, aculeate with cylindrical spines 1 μ in length, 12–14 μ . . . . *Diacheopsis metallica*

g. Sporangia sessile, ovate, taller than wide . . . . 6. *L. Carestiae*

g. Sporangia stalked, globose or depressed-globose . . . . h

h. Stalks short, stout i

h. Stalks long, slender . . . . k

i. Capillitium delicate, pale, flaccid, spores pale, punctate, 8–11 μ 7. *L. arcyrioides*

i. Capillitium coarse, dark throughout, rigid, spores dark, averaging a little larger . . . . j

j. Spores 10–12 μ, with large scattered spines, capillitium purplish brown throughout . . . . 8. *L. muscorum*

j. Spores 12–15 μ, echinulate, capillitium purplish, with pale tips 9. *L. Sauteri*

k. Columella dividing at apex into several main branches of the capillitium which give rise to the circinate-flexuous capillitial threads 10. *L. arcyrionema*

k. Columella undivided at apex, giving rise directly to the numerous capillitial branches l

l. Capillitium brown throughout, not dense, freely branching and anastomosing; spores smoky-brown, punctate, 11–14 μ . . . . 11. *L. columbinum*

l. Capillitium not brown throughout, sparsely branching and anastomosing . . . . m

m. Spores punctate, 7–9 μ; capillitium typically colorless as it leaves the columella, then abruptly dark with pale tips . . . . 12. *L. scintillans*

m. Spores strongly aculeate, 15–20 μ; capillitium not as above, ranging from black to colorless but tips always colorless and slender 13. *L. echinulatum*

1. LAMPRODERMA CRIBRARIOIDES (Fries) R. E. Fries, Svensk. Bot. Tidskr. **4**: 259. 1911. (FIG. 1, 12)

Stemonitis cribrarioides Fries, Syst. Myc. **3**: 163. 1829.

Lamproderma lycopodii Raunk. Bot. Tidskr. **17**: 90. 1888.

Fructification sporangiate, rarely plasmodiocarpous, clustered or scattered, sessile or short-stalked, diameter 0.8–1.0 mm., total height 1.0–2.0 mm.; peridium purple-brown, iridescent, membranous, wall colorless above, purplish-brown below; stalk, when present, black, often flattened or membranous, 0.1–0.6 mm. high; columella cylindrical, penetrating the sporangium ½–⅔ the height of sporangial cavity, absent in the plasmodiocarpous forms; capillitium a network of pale purplish-brown, flexuous threads which are stouter below, slender and colorless at the tips; spores spherical, dark purplish-brown, regularly and distinctly reticulate with narrow raised bands that form a net with from 8–24 meshes to the hemisphere and that show as a border 0.5–1.5 μ wide, 11–16 μ. Plasmodium not known.

TYPE LOCALITY: Germany.

HABITAT: On pine stumps, dead leaves and twigs and *Lycopodium*.

DISTRIBUTION: Colorado; Great Britain, Europe, Rumania. Mainly alpine.

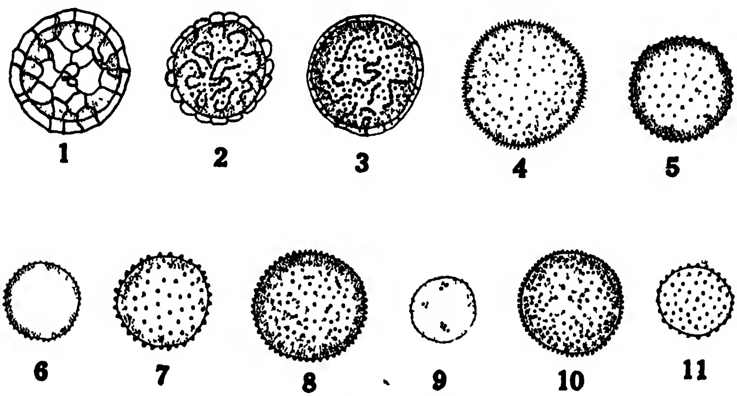
ILLUSTRATIONS: Lister (1925), *pl. 133, figs. a, b, c, d, e;* Macbride and Martin, *pl. XIII, figs. 309, 310.*

This species is easily distinguished by the large dark spores with narrow reticulate bands. G. Lister gives the spore size 11–18 μ, Raunkiaer 12–18 μ, Meylan 11–14 μ; in the collections studied the spores were rather uniformly 14–16 μ. At first sight this species might be confused with *L. Sauteri*, but on microscopical examination the large, distinctly reticulated spores are adequate to separate it from any other *Lamproderma*. *L. cristatum* has spores with warted crests appearing more or less reticulate, and *L. robustum* has warts arranged in lines over a portion of the surface of some of the spores, but those of *L. cribrarioides* are readily distinguished from the spores of either of the other two species.

2. LAMPRODERMA CRISTATUM Meylan, Bull. Soc. Vaud. Sc. Nat. **53**: 457. 1921. (FIG. 2, 13)

Fructification sporangiate, spherical or ovate, sessile or very short stalked, crowded or scattered, diameter 1.0–1.5 mm., total

height 1.5–2.0 mm.; peridium dark gray to iridescent, thin, membranous, evanescent; hypothallus membranous; columella cylindrical, sometimes tapering; capillitium rather pale, gray or purplish, radiating as wavy threads from the columella, frequently anastomosing, colorless at tips; spores globose, dark purplish brown in mass, purple-gray by transmitted light, marked with vesicular warted crests, 12–15 μ. Plasmodium not known.



FIGS. 1–11. Spores, from camera lucida drawings at a magnification of × 1500, reduced in reproduction to × 1000. Fig. 1, *Lamproderma cribrarioides;* 2, *L. cristatum;* 3, *L. robustum;* 4, *L. Gulielmae;* 5, *L. Carestiae;* 6, *L. arcyrioides;* 7, *L. muscorum;* 8, *L. Sauteri;* 9, *L. arcyrionema;* 10, *L. columbinum;* 11, *L. scintillans.*

TYPE LOCALITY: Switzerland.

HABITAT: On leaves, twigs, etc., near melting snow.

DISTRIBUTION: Known only from Switzerland.

ILLUSTRATIONS: Meylan, Bull. Soc. Vaud. Sc. Nat. **53**: 457, *fig. B;* Lister (1925), *pl. 216, fig. h;* Macbride and Martin, *pl. XIII, fig. 311.*

This species has been collected only in the Jura Mountains by Meylan. The specimen examined was authentic material. The spores are very distinct and are unlike those of any other species in the Stemonitaceae. There is no doubt that this is a distinct species. It has not been collected thus far from the United States.

3. LAMPRODERMA ROBUSTUM Ellis & Ev. Bull. Washburn Lab. Nat. Hist. **1**: 5. 1884. (FIG. 3, 14)

Lamproderma atrosporum Meylan, Bull. Soc. Vaud. Sc. Nat. **46**: 51. 1910.

Lamproderma Sauteri Rost. var. *robustum* (Ellis & Ev.) Graff, Mycologia 20: 106. 1928.

Fructification sporangiate, globose to elliptical or obovate, scattered or clustered, stipitate or sessile, diameter 1.0–1.3 mm., total height 1–2 mm.; peridium dark, purple-black with silvery sheen, fugacious, breaking up into small fragments, some of which adhere to the tips of the capillitium; stipe, when present, stout, arising from a distinct membranous hypothallus; columella cylindrical or clavate, slender, attaining one half the height of the sporangial cavity; capillitium of stout, olive-brown or black branching threads, the ends of the branches frequently obviously attached to the peridium by conspicuous enlargements; spores spherical, dark, snuff-brown, strongly and densely verrucose or reticulate by the linear arrangement of the warts over a portion of the surface of some of the spores, 12–15 μ.

TYPE LOCALITY: Mt. Paddo, Washington.

DISTRIBUTION: Washington, Oregon; as *L. atrosporum* in California, Utah, ?Quebec; Switzerland and England.

HABITAT: On woody branches and dead leaves, typically in alpine localities.

ILLUSTRATIONS: Macbride ed. 2 (1922), *pl. V, figs. 4, 4a;* as *L. atrosporum* in Lister (1925), *pl. 133, figs. f, g, h, i,* and in Macbride and Martin (1934), *pl. XIII, figs. 312, 313.*

Comparison of type material of *L. robustum* with authentic material of *L. atrosporum* from Switzerland shows them to be identical in essential respects. Both species possess to a marked degree enlargement of the tips of the capillitial branches by means of which they are attached to the peridium. This character has been held to be a unique diagnostic feature of *L. atrosporum*, but since the other, previously described species possesses it also, together with similar spore size, color and markings, as well as the same general structural and growth characteristics, it seems evident that they represent one and the same species. Since *L. robustum* is the older name it is to be retained and *L. atrosporum* is to be regarded as a synonym.

For years *L. robustum* has been associated with *L. Sauteri* from which it may be distinguished by its dark and distinctly verrucose spores which tend to exhibit some degree of reticulation and its

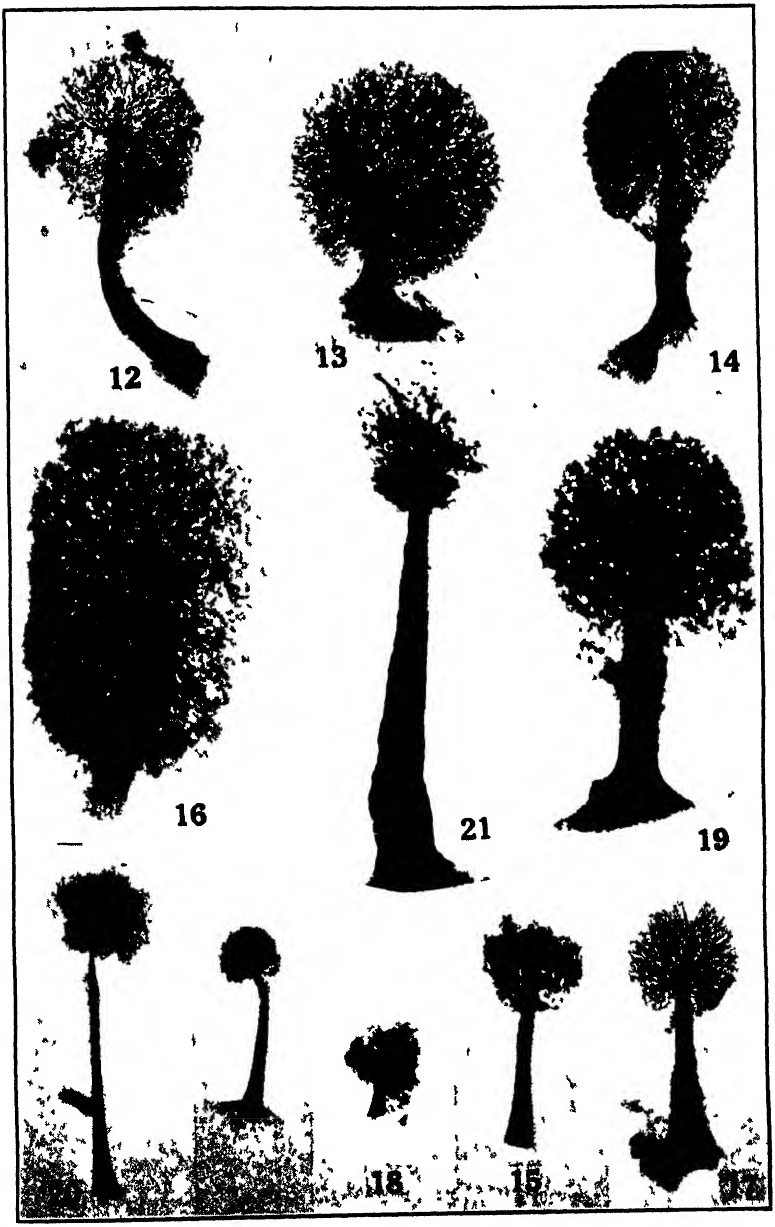
unique enlargements of the capillitial tips. The attachment of the tips of the capillitium to the peridium give to this species a diagnostic character possessed by no other *Lamproderma*. This character suggests relationship between *L. robustum* and *Clastoderma Debaryanum*.

No mention was made of *Lamproderma robustum* by Hagelstein in his recent "Mycetozoa of North America" in spite of the fact it is a species described from North America.

Lister and Howard (Jour. Bot. **57**: 25. 1919) described the variety *debile* of *L. violaceum*, i.e. *L. arcyrioides* of the present treatment, with pale capillitium and pale, spinulose spores 10–11 μ. In the same article (p. 27), the variety *anglicum* of *L. atrosporum* is described with capillitial branchlets that adhere to the sporangial wall and large dark spores, more or less reticulate. A footnote appears in the article stating that Meylan suggests both forms are varieties of *L. atrosporum*. It is rather interesting to note that at this time G. Lister did not agree with Meylan, but in 1925 in the 3rd edition of the English Monograph both forms are treated as varieties of *L. atrosporum*.

No material of either of these forms was available for study. Judging entirely from the description, var. *debile* seems to resemble *L. arcyrioides* much more closely than *L. atrosporum* and if it is worthy of recognition at all, which is believed doubtful, it should be associated with *L. arcyrioides*. Var. *anglicum*, if worthy of recognition, is to be regarded as a variety of *L. robustum*, since *L. atrosporum* is a synonym of that species.

Meylan (Bull. Soc. Vaud. Sc. Nat. **57**: 368. 1932) described two varieties and one form of *L. atrosporum*: var. *macrosporum* with spores 15–18 μ; var. *echinulatum* with spores covered with long papillae; form *subcylindricum* with slender sporangia 2–3 mm. high. No material of these varieties was available for study, but on the basis of the meager descriptions it is considered very doubtful whether they represent more than growth forms which have developed in response to environmental conditions. Since the name *L. atrosporum* has been reduced to synonymy, these so-called varieties would, if recognized, be varieties of *L. robustum*, the valid name for the species.



Figs. 12–22. Photomicrographs of sporangia × 24. Fig. 12, *Lamproderma cribrarioides;* 13, *L. cristatum;* 14, *L. robustum;* 15, *L. Gulielmae;* 16, *L. Carestiae;* 17, *L. arcyrioides;* 18, *L. muscorum,* 19, *L Sauteri;* 20, *L. arcyrionema,* 21, *L. columbinum;* 22, *L. scintillans.*

4. LAMPRODERMA GULIELMAE Meylan, Bull. Soc. Vaud. Sc. Nat. **52**: 449. 1919. (FIG. 4, 15)

Fructification sporangiate, spherical or obovoid, loosely clustered, diameter 0.3–0.5 mm., total height 1.0–2.0 mm.; peridium bluish gray, with metallic luster, dotted with black depressed spots, some of which on dehiscence remain attached to the capillitium; stipe slender, subulate, black, 1–1.2 mm. high; columella extending to ½ the height of the sporangial cavity; capillitium of pale brown, hyaline threads radiating from the apex of the columella; spores spherical, blackish purple, strongly echinulate, 12–15 μ. Plasmodium translucent yellow (Brandza).

TYPE LOCALITY: Switzerland.

HABITAT: On dead leaves of beech and needles of conifers.

DISTRIBUTION: Colorado; Switzerland, England, Moldavia.

ILLUSTRATIONS: Lister (1925), *pl. 215, figs. a, b, c, d;* Macbride and Martin, *pl. XIII, figs. 314, 315;* Hagelstein, *pl. 12, fig. 2.*

A unique species, recognizable at once. The black depressed spots on the otherwise silvery blue peridium distinguish it from *L. echinulatum*, in which the spores are quite similar in marking but somewhat larger in size.

The only American collections known are two from Colorado by W. C. Sturgis.

5. LAMPRODERMA INSESSUM G. List. Trans. Brit. Myc. Soc. **4**: 41. 1912.

Fructification sporangiate, sessile, clustered, sub-globose or forming short plasmodiocarps, 0.8–1.0 mm. in diameter; peridium dark, purple-brown, with iridescent reflections, membranous; columella lacking; capillitium scanty, simple or sparingly branched, of pale purple threads, sometimes with axillary expansions and bead-like thickenings; spores spherical, dark brownish purple, closely echinulate, 18–19 μ. Plasmodium unknown.

TYPE LOCALITY: Scotland.

HABITAT: On lichen, on trunk of a living sycamore.

DISTRIBUTION: Known only from a single collection.

ILLUSTRATIONS: Lister, Trans. Brit. Myc. Soc. **4**: 1912, *pl. 1, figs. 2, 2a, 2b;* Lister (1925), *pl. 215, figs. e, f.*

Lister proposed the name *Lamproderma insessum* for this species lacking a columella, but in all other respects a *Lamproderma.* The genus *Diacheopsis* was established by Meylan in 1930 to

accommodate a species closely related to *Diachea* and *Lamproderma* but likewise lacking a columella. Exteriorly it resembles *Diachea*, while its interior composition is similar to *Lamproderma*, from which it is distinguished almost entirely on the lack of a columella. One species was proposed, *Diacheopsis metallica*. Macbride and Martin suggested that *Lamproderma insessum* might be transferred to the genus *Diacheopsis*, but did not actually propose the combination.

Lamproderma insessum is slightly smaller in diameter than *Diacheopsis metallica*, its spores are closely echinulate and much larger, 18–19 μ. In growth habit, color of peridium, shape, and absence of a columella both species are obviously close, and should be regarded as congeneric.

6. LAMPRODERMA CARESTIAE (Ces. & de Not.) Meylan, Bull. Soc. Vaud. Sc. Nat. **57**: 368. 1932. (FIG. 5, 16)

Stemonitis Carestiae Ces. & de Not. Erb. Crit. Ital. No. 88. 1879.

Lamproderma violaceum Rost. var. *Carestiae* List. Mycetozoa 130. 1894.

Lamproderma Sauteri Rost. var. *Carestiae* Meylan, Bull. Soc. Vaud. Sc. Nat. **51**: 264. 1917.

Fructification sporangiate, globose or ovoid, sessile or rarely short stalked, diameter 0.9–1.3 mm.; total height 1.0–1.5 mm.; peridium violet-blue with metallic luster; columella cylindrical, about ½ the height of the sporangial cavity; capillitium dark, purple-brown or black, colorless at tips, dense; spores spherical, dark, punctate, 10–12 μ. Plasmodium not known.

TYPE LOCALITY: Italy.

HABITAT: On turf and hollow herbaceous stalks in alpine situations.

DISTRIBUTION: Oregon, California; Scotland, Sweden, Germany, Switzerland and North Italy.

ILLUSTRATIONS: Lister (1925), *pl. 132, figs. h, i, k, l* (as *L. violaceum* var. *Carestiae*); Macbride and Martin, *pl. XIII, figs. 316, 317*.

In the English Monograph this species is regarded as a variety of *L. violaceum*, which is itself here regarded as a synonym of *L. arcyrioides*. *L. Carestiae* differs from *L. arcyrioides* by its

elongate sessile sporangia, its dense, dark capillitium and its distinctly larger spores. *L. Carestiae* is to be distinguished from *L. Sauteri* by its sessile, ovate sporangia, its dense, dark and rather rigid capillitium and its pale, smaller spores.

L. arcyrioides, *L. Sauteri* and *L. Carestiae* are quite obviously closely related but sufficiently distinct and uniform to be regarded as separate species.

7. LAMPRODERMA ARCYRIOIDES (Somm.) Rost. Mon. 206. 1874. (FIG. 6, 17)

Stemonitis arcyrioides Somm. Mag. for Naturvidensk. **7**: 298. 1827.

Stemonitis violacea Fries, Syst. Myc. **3**: 162. 1829, not Roth 1788, nor Schum. 1803.

Lamproderma violaceum (Fries) Rost. Versuch 7. 1873.

?*Lamproderma leucosporum* Rost. Mon. App. 26. 1876.

Lamproderma nigrescens Sacc. Michelia **2**: 262. 1882, not Rost. 1874.

?*Lamproderma tatricum* Racib. Hedw. **28**: 117. 1889.

Lamproderma Saccardianum Massee, Mon. 101. 1892.

Tilmadoche Berkeleyi Massee, Mon. 332. 1892.

Fructification sporangiate, closely gregarious or scattered, depressed globose, somewhat umbilicate below, sessile or short stipitate, erect, diameter 0.3–1.0 mm.; total height 0.6–1.5 mm.; peridium shining with metallic blue or purple iridescent reflections; stalk, when present, stout, black, even, varying from very short to 1½ times the height of the sporangium; hypothallus membranous, red-brown; columella cylindrical or tapering toward the apex, ⅓–⅔ the height of the sporangial cavity; capillitium of lax and flaccid, flexuous threads, branching and anastomosing to form a dense net-work, pale brown as they leave the columella, becoming pale again at the tips; spores spherical, violaceous to purplish gray, minutely punctate, 8–11 μ.

TYPE LOCALITY: Norway.

HABITAT: On old wood, decaying sticks and leaves.

DISTRIBUTION: Common in the United States; England, Scotland, Wales, France, Germany, Switzerland, Norway, Portugal, Tasmania.

ILLUSTRATIONS: Rost. Mon. *pl. IV, fig. 64;* Morgan, Jour. Cin. Soc. Nat. Hist. **16**: *pl. XI, fig. 27* (as *L. violaceum*); Lister (1925),

pl. 132, figs. a, b, c, d, e; Crowder, Nat. Geo. Mag. **49**: *pl. X* (as *L. violaceum*); Baker, Univ. Iowa Stud. Nat. Hist. **14**: *pl. VI, fig. 49* (as *L. violaceum*); Macbride and Martin, *pl. XIII, figs. 318, 319* (as *L. violaceum*).

This species is recognized by its pale, lax, capillitium made up of flexuous threads which anastomose freely. The capillitium tends to be pale as it leaves the columella becoming colorless at the tips. *L. scintillans* is to be distinguished from *L. arcyrioides* by its dense, rigid and sparingly branched capillitial threads, its long thin stipe and smaller but more distinctly marked spores.

In the English Monograph (1925) *L. Sauteri* and *L. Carestiae* are treated as varieties of *L. violaceum.* I regard them as distinct species and will discuss them fully as such. The name *Lamproderma violaceum* (Fries) Rost. has been generally accepted for this species. However, if the rule of priority is adhered to, it is invalid and *L. arcyrioides* becomes the valid name.

8. LAMPRODERMA MUSCORUM (Lév.) Hagelstein, Mycologia **27**: 88. 1935. (FIG. 7, 18)

Enerthenema muscorum Lév. Ann. Sci. Nat. IV. **20**: 289. 1863.

Fructification sporangiate, scattered, globose, diameter 0.3–0.5 mm., total height 0.6–1.0 mm.; peridium blue or bronze, iridescent, thin, membranous, more or less persistent at base; stalk subulate, setaceous, black, shining, about ½ the total height, arising from a circular, purple-brown hypothallus; columella thick, tapering to the obtuse end, extending half-way into the sporangial cavity; capillitium dense, of rigid threads radiating in all directions from the apex of the columella, dichotomously forking and branching, purple-brown from base to tips; spores spherical, violet-brown, strongly echinulate, 10–12 μ. Plasmodium not known.

TYPE LOCALITY: Colombia (New Granada).

HABITAT: On dead leaves.

DISTRIBUTION: Colombia; New York and Pennsylvania.

ILLUSTRATIONS: Mycologia **27**: 87 (*figs. 1–3*), 1935; Hagelstein (1944), *pl. 4, figs. 1, 2, 3, 4.*

This species is close to *L. scintillans* but is distinct by reason of its continuous, dark capillitium, its larger and coarsely echinu-

late spores and its shorter and stockier growth habit. In the latter respect it resembles *L. arcyrioides* but the spores and capillitium are completely different.

9. LAMPRODERMA SAUTERI Rost. Mon. 205. 1874. (FIG. 8, 19)
Lamproderma violaceum (Fries) Rost. var. *Sauteri* (Rost.) List. Mycetozoa 129. 1894.

Fructification sporangiate, globose to slightly flattened, umbilicate below, diameter 1–2 mm., total height 1 4 mm.; peridium dark blue, with metallic luster, not brilliant, membranous, persistent; stipe usually short, rarely exceeding the height of the sporangium, black, subulate, from a firm, well developed hypothallus; columella cylindrical, truncate ½ height of sporangial cavity; capillitium dark, purplish or brown, threads coarse, densely branched, forming a compact network, the tips of which appear hoary after the spores are shed; spores spherical, purplish brown, echinulate 12–15 μ.

TYPE LOCALITY: Austria (Salzburg).

HABITAT: On turf and hollow herbaceous stalks, typically in alpine localities.

DISTRIBUTION: Washington, Oregon, California, Montana, Colorado, Michigan, Ontario; Scotland, Sweden, Germany, North Italy.

ILLUSTRATIONS: Rost. Mon. *pl. XIII, fig. 5;* Lister (1925), *pl. 132, figs. f, g, m* (as *L. violaceum* var. *Sauteri*); Macbride and Martin, *pl. XIII, figs. 320, 321.*

This species is distinguished from *L. arcyrioides* (*L. violaceum*), of which Lister regards it as a variety, by the more robust sporangia, and the larger, darker and more distinctly spinulose spores. *L. Sauteri* is distinguished from *L. Carestiae* by its stipitate habit, its coarse, purplish capillitium and its darker, echinulate spores which average a little larger.

The shape and color of the sporangia are variable characters which have led unjustifiably to the naming of new varieties of this species. Spore characters, such as size, marking and color, are considerably more constant and more emphasis should be placed upon them than on the shape and color characters of the entire fructification. Spore characters appear to be less affected by varying conditions in the environment during maturation

than external features such as color, shape and size of fructification and even than capillitial characters, and species, varieties or forms described on the basis of such superficial differences should be recognized with great caution.

In 1925 Meylan (Bull. Soc. Vaud. Sc. Nat. **56**: 71) described a variety *piriforme* of *L. Sauteri* with dark spores much larger than those of the type, 15–18 μ, and spinulose. In 1932 he erected a new species, *L. ovoideum* (Bull. Soc. Vaud. Sc. Nat. **57**: 373. 1932). In the same publication he states that the variety *piriforme* which he originally associated with *L. Sauteri*, has nothing in common with that species and would have been regarded as a separate species except that he already established a new species, *L. ovoideum*, of which *piriforme* could be considered a variety. A specimen from Meylan labelled *L. piriforme* was examined. In the literature available no reference to such a species can be found; it is possible that this specimen was distributed during the time Meylan was undecided as to its proper position, and that later he decided to make it a variety of *L. ovoideum*, hence never published the name *L. piriforme*. The specimen examined seems to be closer to *L. echinulatum* than to *L. Sauteri* and will be fully discussed under that species.

Four other varieties and two forms of *L. Sauteri* have been described by Meylan. They will be listed and comments concerning the distinctive features will be made in so far as is possible but unfortunately material of only one variety was available for study. Var. *brunnescens* (Bull. Soc. Vaud. Sc. Nat. **56**: 325. 1927) is described as having brown or dark brown, shining sporangia, generally without iridescent reflections, pale capillitium and pale spores which are almost smooth, 9–11 μ. In the absence of any material it is impossible to discuss this variety adequately, but on the basis of the description, it is possible that it represents an aberrant form of *L. arcyrioides*, inasmuch as the characters listed, with the exception of the color of the sporangia, are remarkably similar to those of *L. arcyrioides*. Var. *atrogriseum* (Bull. Soc. Vaud. Sc. Nat. **57**: 366. 1932) was described as having a dull, iron-gray peridium, and spores 15–18 μ in diameter, but the spores examined from an authentic specimen from Meylan are consistently 15 μ in size. On the basis of the

one collection seen, this variety is regarded as of doubtful significance, since it is too close to *L. Sauteri* and probably represents only a response to environmental conditions. Var. *pulchrum* (Bull. Soc. Vaud. Sc. Nat. **57**: 366. 1932) is described as having a shining, metallic peridium, a denser and darker capillitium than the typical form, and spores 15–18 μ. There was no material available for study of this variety, but on the basis of its meager description, it may be regarded as doubtful. Var. *fallax* Meylan (Bull. Soc. Vaud. Sc. Nat. **58**: 320. 1935) is distinguished by its whitish or slightly rose-colored capillitium. Meylan regards it as a form parallel to var. *leucotrichum* of *L. splendens*.

The two forms described by Meylan (Bull. Soc. Vaud. Sci. Nat. **57**: 366. 1932) are *gracile*, with stalks exceeding somewhat the height of the sporangium, and *turbinatum*, with top-shaped sporangia. Both seem to represent growth responses, and in the absence of authentic material and on the basis of the descriptions these two forms are to be regarded as of doubtful significance.

10. LAMPRODERMA ARCYRIONEMA Rost. Mon. 208. 1874. (FIG. 9, 20)

?*Lamproderma minutum* Rost. Mon. App. 26. 1876.

?*Lamproderma suboeneum* Massee, Mon. 95. 1892.

Comatricha Shimekiana Macbride, Bull. Lab. Nat. Hist. Iowa **2**: 380. 1893.

?*Lamproderma inconspicuum* Schroet. Hedw. **35**: 208. 1896.

Fructification sporangiate, globose, scattered or gregarious, diameter 0.5–0.75 mm., total height 1–2.5 mm.; peridium silvery gray or bronze, iridescent, shining, thin, membranous, persistent, especially as a calyculus at base of sporangium; stipe erect, long, ⅔–¾ total height, subulate-setaceous, slender, hairlike, rigid, black; columella cylindrical, slender, smooth, attaining ⅓–½ total height of sporangial cavity, then dividing into the primary branches of the capillitium; capillitium purple-brown, slender, of intricately circinate-flexuous threads, branching repeatedly and anastomosing to form a close network with few free ultimate branches; spores spherical, jet black in mass, pale violaceous by transmitted light, minutely punctate, 6–8 μ. Plasmodium watery white.

TYPE LOCALITY: Europe.

HABITAT: On dead leaves.

DISTRIBUTION: Common in United States, reported from Canada to Nicaragua, Puerto Rico, Brazil; Europe, Asia and Africa. Uncommon in England.

ILLUSTRATIONS: Bull. Lab. Nat. Hist. Iowa **2**: *pl. 10, figs. 3, 3a, 3b* (as *Comatricha Shimekiana*); Jour. Cin. Soc. Nat. Hist. **16**: *pl. 11, fig. 26;* Lister (1925), *pl. 129;* Crowder, Nat. Geog. Mag. 49: *pl. 15;* Baker, Univ. Iowa Stud. Nat. Hist. **14**: *pl. 6, fig. 48;* Macbride and Martin, *pl. XIII, figs. 322, 323;* Hattori (1935), *pl. 13, fig. 4;* Hagelstein (1944), *pl. 16, fig. 9.*

In typical specimens this species may be readily recognized because of the peculiar apical divisions of the columella. Among Lamprodermas this condition is unique. Ordinarily the columella is undivided except at the apex, but specimens have been seen in which the columella branched directly above the base of the peridium. The stipe tends to be long, but varies even within a single fruiting. The spores are rather constant in size and markings, being lightly punctate all over, but sometimes with patches in which the markings appear somewhat da,ker and larger.

The branching of the apex of the columella of this species resembles closely that found in the columellae of several species of *Comatricha*. The two genera *Lamproderma* and *Comatricha* are admittedly closely related; however, in *Lamproderma* the peridium is consistently more persistent and shines with metallic iridescence. This constitutes, at least temporarily, a convenient means of distinguishing the two genera.

Var. *japonicum* Meylan (Bull. Soc. Vaud. Sc. Nat. **58**: 323. 1935) differs from the species in its robust stature, lax capillitium and spores 8–9 μ in diameter. Lister (1925) mentions a variety similarly characterized but does not name it.

11. LAMPRODERMA COLUMBINUM (Pers.) Rost. Versuch 7. 1873. (FIG. 10, 21)

Physarum columbinum Pers. Ust. Ann. Bot. **15**: 5. 1795.

Trichia physaroides Schum. Enum. Pl. Saell. **2**: 210. 1803.

Stemonitis physaroides Alb. & Schw. Consp. Fung. 103. 1805.

Trichia columbina (Pers.) Poiret, Lam. Encyl. **8**: 52. 1808.

Fulgia encaustica Chev. Fl. Par. ed. 2, 347. 1836.
Lamproderma physaroides (Alb. & Schw.) Rost. Mon. 202. 1874.
?*Lamproderma Schimperi* Rost. Mon. 203. 1874.
Lamproderma iridescens (Berk.) Rost. Mon. App. 25. 1876.
?*Lamproderma Staszycii* Racib. Hedw. **28**: 116. 1889.
Lamproderma Cruchetii Meylan, Bull. Soc. Vaud. Sc. Nat. **52**: 96. 1918.
Lamproderma brevipes Meylan, Bull. Soc. Vaud. Sc. Nat. **56**: 322. 1927.
Lamproderma subglobosum Meylan, Bull. Soc. Vaud. Sc. Nat. **56**: 322. 1927.

Fructification sporangiate, globose or ellipsoid, scattered or gregarious, 0.5–1.0 mm. in diameter, total height 2–3 mm.; peridium rich violet or purple with metallic iridescence, membranous, persistent; stalk long, usually about ¾ the total height, black, straight, subulate; columella cylindrical with a conical apex, or clavate, ⅓–½ the height of the sporangial cavity; capillitium of brownish purple threads, arising from nearly all parts of the columella, rigid, sparingly forked for about ½–⅔ their length, then anastomosing freely to form a large-meshed open network; spores spherical, smoky-brown, punctate, 11 -14 μ. Plasmodium white, rarely yellow (Lister).

TYPE LOCALITY: Europe.

HABITAT: On coniferous wood, mossy stumps, logs and rocks.

DISTRIBUTION: Common in the United States east of the Mississippi river and west of the Great Plains; British Columbia, Europe and Tasmania.

ILLUSTRATIONS: Rost. Mon. *pl. IV, fig. 61;* Lister (1925), *pl. 191, figs. a, e, f, g, l, m;* Macbride and Martin, *pl. XIII, figs. 326, 327.*

This species is characterized by its rich, violet-purple, iridescent peridium, its rigid capillitium of dark threads, unforked for about ½ their length, anastomosing peripherally to form a loose-meshed network, somewhat paler in color than the rest of the capillitium, and its smoky-brown, punctate spores. The shape of the sporangium and columella, and the length of the stalk are quite variable but the spore characters appear to be constant. The brown capillitium arising from nearly all parts of

the columella and the larger, punctate brown spores distinguish it from *L. arcyrioides*. From *L. arcyrionema* this species is easily distinguished by the capillitial threads which arise from all parts of the conic columella and the larger and darker spores. *L. scintillans* is distinguished from this species by its generally smaller size, its capillitium, pale as it leaves the columella, and its smaller spores.

G. Lister has described three varieties of this species. Var. *gracile* is distinguished by a long, slender, curved stalk, 5–6 times as long as the sporangium. One authentic specimen from Meylan and several specimens similar in character from the western United States have been examined critically and it is concluded that these specimens represent growth responses to environmental conditions at the time of fruiting and as such are not worthy of varietal distinction, inasmuch as they exhibit only differences of size and shape. Such differences as these are well within the realm of possibility and may occur in a single collection containing numerous individual sporangia formed from the same plasmodium. Var. *brevipes*, with short, slender stalks and dark capillitium often knotted with irregular expansions at the axils of the branches, was raised to specific status by Meylan. Referring to the three varieties *gracile*, *brevipes*, and *iridescens*, G. Lister says: "All these forms appear to merge into one another and defy attempts to divide them into distinct species." No authentic material of var. *iridescens* was available for this study. Inasmuch as G. Lister admits the three varieties of *L. columbinum* merge into one another, the validity of this variety is also open to question. It would seem advantageous to recognize them as growth forms rather than varieties.

G. Lister does not regard Meylan's species *L. Cruchetii* as worthy of specific distinction since it is based largely on plasmodial color. Other minor differences are noted by Meylan, but an examination of authentic material reveals its relationships with *L. columbinum* as too close for specific distinction.

L. subglobosum Meylan is here regarded as synonymous with *L. columbinum;* a flattened sporangium on a long stalk with a short columella is insufficient reason to give it specific rank. The spore characters are remarkably similar to *L. columbinum.*

Authentic material from Meylan was examined as well as a specimen of Brandza's from Rumania. Four specimens from Oregon were also examined which externally appeared to be *L. subglobosum*, but they too proved to be *L. columbinum*.

Lamproderma physaroides (Alb. & Schw.) Rost. is doubtfully included with *L. columbinum* by Lister. Macbride and Martin believed it to be a good species on the basis of its description by Rostafinski in his Monograph, but specimens reported as such from North America have proved to be *L. columbinum*. Hagelstein includes it with *L. columbinum* without comment. In the absence of authentic material and because the description in Macbride and Martin coincides so closely with that of *L. columbinum* I am inclined to regard the names as synonymous.

12. LAMPRODERMA SCINTILLANS (Berk. & Br.) Morgan, Jour. Cin. Soc. Nat. Hist. **16**: 131. 1894. (FIG. 11, 22)

Stemonitis scintillans Berk. & Br. Jour. Linn. Soc. **15**: 84. 1876.

Lamproderma arcyrioides (Somm.) Rost. var. *iridea* Cooke, Myx. G. B. 50. 1877.

Lamproderma irideum (Cooke) Massee, Mon. 95. 1892.

Fructification sporangiate, scattered or gregarious, globose to depressed-globose, diameter 0.3–0.5 mm., total height 1.5–2.0 mm.; peridium metallic blue-purple, brilliantly iridescent, membranous, persistent; stalk brown or black, shining, nodding or erect, long, slender, even; columella cylindrical, truncate, scarcely attaining ½ the height of the sporangial cavity; capillitium of dense, rigid, furcate, straight, dichotomously branched brown threads which anastomose ½–⅓ the length of the threads and are typically colorless as they leave the columella; spores spherical, violet-gray, punctate, 7–9 μ. Plasmodium not known.

TYPE LOCALITY: Ceylon.

HABITAT: On old leaves and moss especially in early spring.

DISTRIBUTION: Common in the British Isles and Eastern United States; reported from Bolivia, Rumania, Ceylon, Japan and Java.

ILLUSTRATIONS: Morgan, *pl. XI, fig. 28;* Lister (1925), *pl. 130, figs. a, b, c, d, e, f;* Macbride and Martin, *pl. XIII, figs. 324, 325.*

The remarkable capillitium of this species constitutes an easy diagnostic character. It is very rigid and unbranched or unanastomosed until from ½–⅔ the distance from the columella. As compared with *L. arcyrioides* the threads are coarser and darker in color, but both species exhibit the paleness of the capillitial threads at the apex of the columella. The spores are smaller but more distinctly marked. The stalk is usually about twice as long as in *L. arcyrioides*, but this character is variable.

13. LAMPRODERMA ECHINULATUM (Berk.) Rost. Mon. App. 25. 1876.

Stemonitis echinulata Berk. In Hooker Fl. Tasm. **2**: 268. 1860.

Lamproderma Listeri Massee, Mon. 97. 1892.

Fructification sporangiate, globose, loosely clustered, diameter 0.5–1.0 mm.; total height 2 4 mm.; peridium shining, steel-blue, with gray or green iridescence, membranous, persistent; stalk cylindrical or subulate, black, 1-2.7 mm. high; columella cylindrical, obtuse, ½ height of sporangial cavity; capillitium arising mainly from apex of columella, stout, sparingly forked and anastomosing, purplish-brown to colorless at tips; spores spherical, dark gray or brownish purple, strongly aculeate 15-20 μ. Plasmodium opaque white.

TYPE LOCALITY: Tasmania.

HABITAT: On dead wood.

DISTRIBUTION: Tasmania, New Zealand, Sweden, England, Ireland and Japan.

ILLUSTRATIONS: Jour. Bot. **29**: 1891, *pl. 310, fig. 2*; Lister (1925), *pl. 134, figs. a–i, k;* Hattori, *pl. 13, fig. 6.*

No material of this species was available for study, but on the basis of its description it may be regarded as valid.

A specimen from Meylan labeled *Lamproderma piriforme* was examined. No reference to such a species can be found in the literature. It is possible that this specimen is what he described as *L. ovoideum* var. *piriforme* (Bull. Soc. Vaud. Sc. Nat. **57**: 373. 1932). This specimen has decidedly aculeate spores which are dark and fall well within the size range given for *L. echinulatum*, 15–18 μ. The capillitium is dark, stout, and densely branched with pale tips. The columella attains a little over ½ the height

of the sporangial cavity, as described for *L. echinulatum*, but this is frequently a variable character in the genus. The shape of the sporangia of *L. echinulatum* is given as globose, while that of the variety under discussion is more ovate or piriforme. These two descriptions seem not to coincide too closely, but as sporangial shape is known to be a variable character and therefore not as important as the more constant and uniform spore characters they are regarded as of much less significance.

The suggestion is made here that, since *L. ovoideum* Meylan var. *piriforme* Meylan is so close to *Lamproderma echinulatum* the former named species be included in the latter, at least until material of the two forms is available for study.

DOUBTFUL SPECIES

LAMPRODERMA ECHINOSPORUM Meylan, Bull. Soc. Vaud. Sc. Nat. 55: 241. 1924.

Fructification sporangiate, spherical or ovoid, sessile or rarely stalked, 1 mm. in diameter; peridium dark brown or grayish, lacking iridescence, dull, persistent, membranous, furrowed or wrinkled; columella ½–¾ the height of sporangial cavity; capillitium usually dark violaceous brown; spores spherical, purple-black, covered with pointed or obtuse spines 1 μ in length, 14–16 μ. Plasmodium not known.

TYPE LOCALITY: Switzerland.

HABITAT: On vegetable debris exposed by melting snow, high in the mountains.

DISTRIBUTION: Known only from Switzerland.

By Meylan this species is regarded as close to *L. atrosporum* (*L. robustum* of this treatment) from which it is distinguished by its persistent brown peridium, and its strongly spinulose but not reticulate spores. From *L. echinulatum* this species is said to be distinguished by its dull colors, sessile habit and somewhat smaller spores.

There was no material of this species available for study, but on the basis of the original description it seems to be very close to *L. echinulatum*, which is the older name and would be the valid one if the two are found to be the same.

LAMPRODERMA FUSCATUM Meylan, Bull. Soc. Vaud. Sc. Nat. **57**: 372. 1932.

Fructification sporangiate, globose, stipitate, diameter about 1 mm., 1–1.5 mm. in total height; peridium gray, with metallic tints of blue or brown, fragile, evanescent; stalk shiny, dark brown, shorter than sporangium, on a conspicuous hypothallus; columella attaining not more than ½ the height of sporangial cavity; capillitium dense, ferruginous; spores spherical to ovate, dark ferruginous in mass, pale by transmitted light, with a distinct lighter area on one side, punctate, 9–11 μ. Plasmodium not known.

TYPE LOCALITY: Switzerland.

HABITAT: On dead twigs.

DISTRIBUTION: Known only from Switzerland.

ILLUSTRATIONS: Bull. Soc. Vaud. Sc. Nat. **57**: 370. 1932. *fig. c.*

Meylan regarded this species as close to *L. atrosporum* (*L. robustum* of the present treatment) because of its fragile peridium which breaks up into fragments. Macbride and Martin suggested it was close to *L. violaceum* (*L. arcyrioides* of this treatment) with which it is obviously associated. Because the material available for study was limited to a single authentic collection, it seems advisable to consider it as a variant of *L. arcyrioides*, at least temporarily, pending further material for study.

LAMPRODERMA OVOIDEUM Meylan, Bull. Soc. Vaud. Sc. Nat. **57**: 373. 1932.

Fructification sporangiate, stipitate, ovate, 1.5–2 mm. in height, 1–1.5 mm. in diameter, dark blue-black, iridescent, especially at the summit, sometimes bronze, shining; stipe short, less than half the height of the sporangium; capillitium dense, dark, brownish purple; spores spherical, dark, papillate, 13–15 μ. Plasmodium white.

TYPE LOCALITY: Switzerland.

HABITAT: On forest litter in alpine localities.

DISTRIBUTION: Known only from Switzerland.

Meylan says this species differs in every respect from *L. Carestiae*, and has in common with *L. Sauteri* only the markings of the spores. In this treatment, spore markings are regarded

as very important and more emphasis is placed on them as criteria for speciation than on external characters which are more subject to changing environmental conditions. Meylan says the spores of this species are papillate, and the spores of *L. Sauteri* are known to be echinulate. This may be a significant difference, or it may be simply a difference in interpretation of meaning of the two terms, consequently in the absence of material for verification the species is regarded as doubtful, for from the description it would seem to be very close to *L. Sauteri*.

Var. *cucumer* Meylan (Bull. Soc. Vaud. Sc. Nat. **57**: 367. 1932) is unquestionably a growth form of *L. Carestiae*. The rather large, dark and indistinctly marked spores, 10–13 μ, place them together at once. The capillitial characters are also quite similar; both have a dense, dark, much branched capillitium which is pale at the tips. The shape of the sporangia is quite variable in the two collections of authentic material studied of var. *cucumer*, ranging from sessile and ovate sporangia to distinctly stalked and cylindrical or cucumber-shaped sporangia. In the authentic material of *L. Carestiae* examined the shape of the sessile sporangia ranged from globose to ovate.

It is highly possible that both the species itself, *L. ovoideum*, and the var. *cucumer* represent growth forms of *L. Carestiae* rather than *L. Sauteri* as suggested for *L. ovoideum*, but until authentic material of *L. ovoideum* is available it may be regarded from the description as close to *L. Sauteri*, while the var. *cucumer* is close to *L. Carestiae*.

In the Lister Monograph and in Hagelstein both *L. Carestiae* and *L. Sauteri* are considered as varieties of *L. violaceum*, *L. arcyrioides* of this treatment. Neither *L. ovoideum* nor its variety *cucumer* exhibit any characters which might associate them with *L. arcyrioides*. This seems to strengthen somewhat the separation of *L. Carestiae* and *L. Sauteri* as distinct species from *L. arcyrioides*.

LAMPRODERMA SPLENDENS Meylan, Bull. Soc. Vaud. Sc. Nat. **57**: **44**. 1929.

Fructification sporangiate, stipitate, rarely sessile, sub-spherical, not umbilicate at the base, 0.8–1.0 mm. in diameter, 1–2 mm.

in total height; peridium dark blue or bronze with brilliant, metallic luster, rarely ashy violaceous or brilliant black; stipe 0.5–0.8 mm. high, black; columella short, thick; capillitium of coarse, rigid, filaments sparsely branched in the interior, densely branched toward the periphery, or sometimes densely branched throughout; spores spherical, pale, punctate, 10–12 μ. Plasmodium white.

TYPE LOCALITY: Switzerland.

HABITAT: On plant debris, at the edge of the melting snows. Alpine.

DISTRIBUTION: Known only from Switzerland.

Critical examination of an authentic collection suggests that this species is too close to *L. Sauteri* to warrant specific distinction. It is here regarded as doubtful.

Var. *leucotrichum* was described by Meylan (Bull. Soc. Vaud. Sc. Nat. **57**: 367. 1932) as having colorless capillitium appearing white.

Form *gracile* was described in the same publication as having a thin stipe, at least equal to the height of the sporangium.

LAMPRODERMA PULCHELLUM Meylan, Bull. Soc. Vaud. Sc. Nat. **57**: 369. 1932.

Fructification sporangiate, sessile, or rarely short stalked, globose, 0.5–1.0 mm. in diameter; peridium dark violet-blue, iridescent, persistent; columella short, sometimes almost lacking, never over ⅓ the height of the sporangial cavity; capillitium densely branched, pale rose; spores spherical, brownish purple, minutely punctate, 12–14 μ. Plasmodium unknown.

TYPE LOCALITY: Switzerland.

HABITAT: On stems of grasses, in characteristic rows. Alpine.

DISTRIBUTION: Known only from Switzerland.

This species seems to be very close to *L. Carestiae*, from which it differs only in its pale capillitium. A color difference unaccompanied by other more significant differences is not here regarded as just reason for speciation. One authentic collection was available for study. It seems justifiable to include this species in *L. Carestiae*, but pending further study and more material it is listed as doubtful.

EXCLUDED SPECIES

1. LAMPRODERMA ELLISIANA Cooke. Possibly *Comatricha laxa*, but certainly not a *Lamproderma*.
2. LAMPRODERMA FUCKELIANUM Rost. Not a *Lamproderma*. Lister says (p. 104, ed. 3) this is *Diachea subsessilis*, which is verified by her figure.
3. LAMPRODERMA HOOKERI (Berk.) Rost. Not a *Lamproderma*, possibly *Badhamia rubiginosa* var. *globosa* according to Lister (p. 19, ed. 3).

DEPARTMENT OF PLANT SCIENCE,
VASSAR COLLEGE,
POUGHKEEPSIE, NEW YORK

PHLYCTOCHYTRIUM AURELIAE PARASITIZED BY RHIZOPHYDIUM CHYTRIOPHAGUM[1]

LIBERO AJELLO[2]

(WITH 28 FIGURES)

In decaying vegetable debris collected from a quiet stream at Lake Minnewaska, Ulster County, New York, in September 1941 and June 1942 two new chytrids were found. They are of especial interest because one is parasitic upon the other, and the host is marked by unusual sporangial ornamentation. The host alone had previously been observed by Dr. Karling among material collected from the Chickahominy River in Virginia and it was recovered by the author in October 1941 and in June 1942 from a bog on Bearfort Mountain, Passaic County, New Jersey, and by Miss Hanson from material collected in Vermont in July 1942.

The parasite produces no marked hypertrophy of the host, nor does it induce septation or other abnormalities. On the contrary, the host may continue developing and produce zoospores under certain conditions even though parasitized. Death of the host seems to occur only when it is attacked early in development or by more than one parasite.

The parasitic chytrid is extramatrical, eucarpic and rhizidiaceous. Its absorbing system is much reduced, consisting merely of a haustorium with two short lateral extensions. Spherical sporangia are formed which dehisce through a rupture of the sporangial wall, liberating small, unigutullate, posteriorally uniflagellate zoospores. Golden-brown resting spores, which upon germination act as prosporangia, have also been observed. These characters place the chytrid in the genus *Rhizophydium*

[1] The writer is indebted to Professor John S. Karling for helpful suggestions and criticism in the course of this study and to Dr. Ludwig Edelstein of The Johns Hopkins Institute of the History of Medicine for the Latin diagnoses.

[2] Present address: The Johns Hopkins Hospital, Box 229, Baltimore 5, Maryland.

and because of its parasitic habit the specific name of *chytriophagum* has been chosen for this aquatic Phycomycete.

The host is epibiotic, monocentric and eucarpic, forming an endobiotic apophysis and a branched rhizoidal system. The inoperculate zoosporangium develops from the persistent epibiotic cyst of the zoospore. The sporangia are covered with numerous hyaline, solid, bipartite teeth. This fungus is therefore considered to be a new species of *Phlyctochytrium* and for personal reasons has been given the specific name of *Aureliae.*

Phlyctochytrium Aureliae is saprophytic, occurring on decaying vegetation and probably on the cast-off integuments of insects. This probability arises from Sparrow's (7) studies on *Asterophlyctis sarcoptoides* Petersen (3) collected in Denmark from insect exuviae. Among the irregularly stellate sporangia of *A. sarcoptoides*, which typically bear scattered over the surface several blunt, refractive protuberances, several atypical sporangia were found. These aberrant sporangia were considered by Sparrow to be either variations of the usual sporangia of *A. sarcoptoides* or the sporangia of an unknown chytrid. This latter suggestion seems to be the correct one, since the host of *Rhizophydium chytriophagum* consistently bears bifurcated teeth and compares favorably with figure 1 k and plate 1, figure 19 in Sparrow's 1937 paper (7). The following quotation from Sparrow's book, "The Aquatic Phycomycetes" (9, p. 296), adds weight to this probability: "The form with a nearly spherical sporangium covered by small solid bipartite spines is very distinct from *Asterophlyctis sarcoptoides*, as further observations of it will no doubt reveal." No sporangia were found in our material having the stellate form and blunt protuberances typical of *A. saroptoides*.

Before describing the life cycle of *Rhizophydium chytriophagum* we will further describe the host.

Phlyctochytrium Aureliae sp. nov.

Sporangia extramatrical, variable in form but predominantly spherical, 12–35 μ in diameter, colorless, covered with numerous hyaline, solid, bicornute teeth, 3.5–4.5 μ long and 3.5 6.5 μ wide, single pronged teeth occasionally formed, tips of teeth at times becoming filiform and elongate, attaining lengths of 20 to 50 μ;

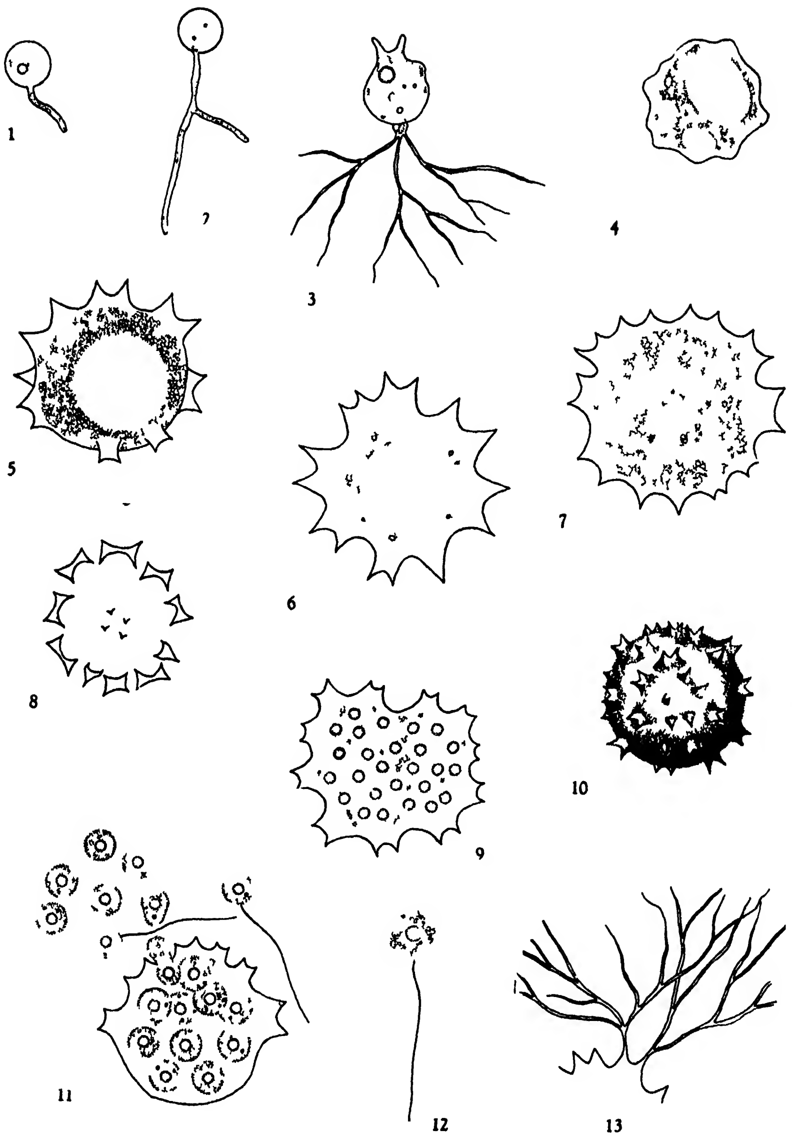
endobiotic system approximately 150 μ long consisting of a spherical apophysis, 3-7 μ in diameter, sometimes irregular or elongate with well developed rhizoids that branch profusely. Zoospores spherical, 4–4.5 μ in diameter, with a single centrally situated refractive globule, 2 μ in diameter and a single posterior flagellum, 15-20 μ long. Resting spores unknown.

Sporangia extramatricalia, formata variatim sed praecipue sphaerica, 12–35 μ diametro, incolorata, oblita dentibus permultis hyalinis solidis, 3.5–4.5 μ longis et 3.5-6.5 μ latis, quorum plurimi bicornes singuli serrati aliquando formantur et quorum summae partes, interdum redactae in forman fili, sunt elongatae crescentes in longitudinem 20-50 μ; systema endobioticum circa 150 μ longum et compositum ex apophysate sphaerica 3-7 μ diametro, non numquam irregulari aut elongata, et ex rhizodeis bene perfectis et ramosissimis. Zoosporae sphaericae, 4-4.5 μ diametro, habentes singulum globulum refractivum 2 μ diametro, quod situm est in medio, et singulum posteriorem flagellum 15–20 μ longum. Sporae perdurantes non observatae.

Saprophytic on decaying vegetation and probably insect exuviae, United States and Denmark (?).

The development of *Phlyctochytrium Aureliae* is essentially similar to the other members of this genus. The thallus develops from the body of the quiescent zoospore, which produces a slender intramatrical germ tube (FIG. 1) that soon branches (FIG. 2) to form the rhizoidal system (FIG. 3). The extramatrical portion—the incipient sporangium increases in size and concomitantly the ornamental teeth begin to appear (FIG. 3). With further development these become increasingly prominent and more numerous (FIG. 5). The rhizoidal system becomes profusely branched and complex and a swelling or apophysis is formed in that portion of the absorbing system immediately below the zoosporangium (FIG. 3). The apophysis may vary in form but is usually spherical and measures 3–7 μ in diameter. The gleaming cytoplasm of the developing sporangium contains vacuoles and numerous scattered droplets of an oil-like substance (FIG. 4). At maturity, the cytoplasm becomes densely granular and the scattered droplets coalesce to form large, more or less regularly spaced refractive globules (FIG. 9). Through cleavage the zoospores are delimited, a single globule being included in each zoospore initial.

Zoospore discharge takes place through a rupture in the sporangial wall, no definite exit papilla being formed. The zoospores



FIGS 1–13 *Phlyctochytrium Aureliae*

emerge en masse, remaining quiescent for varying periods of time, then becoming active and swimming away (FIG 11) The spores are spherical with a long, trailing flagellum and contain a single, centrally situated globule (FIG 12)

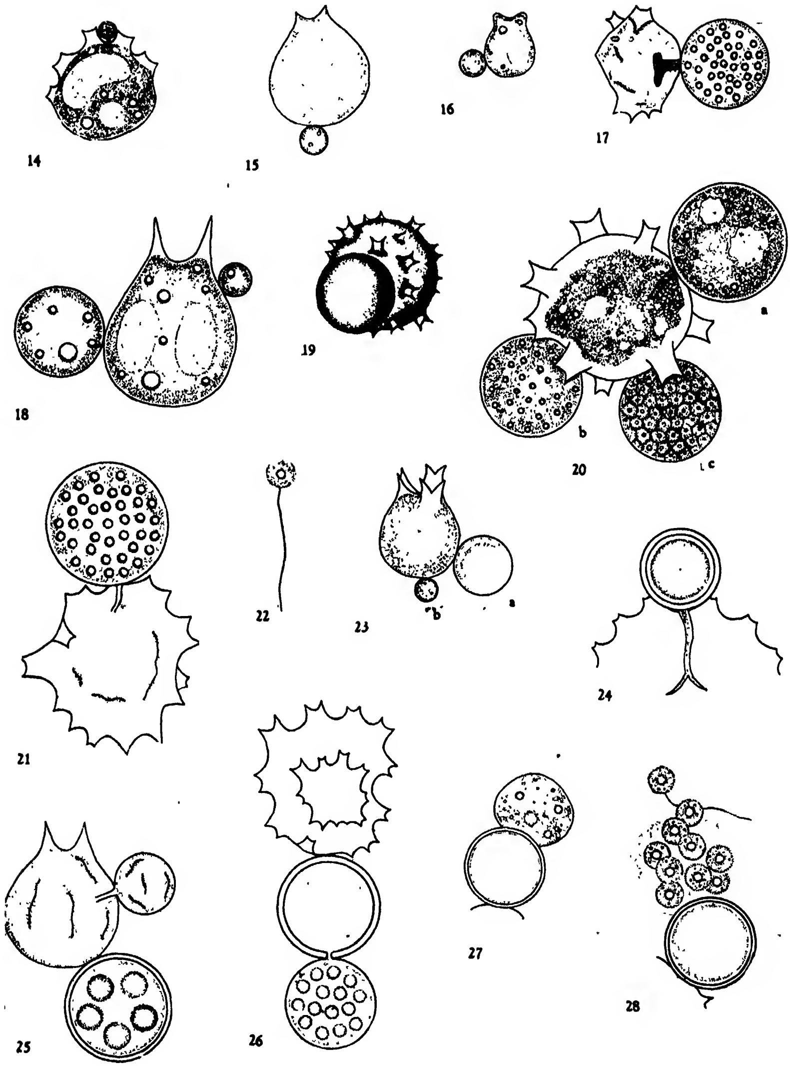
The noteworthy characteristic of *Phlyctochytrium Aureliae* is the sporangial ornamentation. Of the dentigerate species of *Phlyctochytrium*, none have their sporangial surface completely covered with bifurcated teeth. Those species bearing bipartite teeth—*P. Zygnematis* (Rosen) Schroeter, *P. dentatum* (Rosen) de Wildeman, *P. urceolare* Sparrow, and *P. dentiferum* Sparrow—have them arranged in either a single whorl or a double one. The sporangial ornaments of *P. Aureliae* are scattered over the whole surface in an apparently haphazard fashion (FIG. 10). A group of these hyaline bipartite teeth is shown in surface view in figure 8. These teeth are solid, with a concave base and incised and measure 3.5–4.5 μ in length and 3.5–6.5 μ in width. A single pronged tooth is shown with them (FIG. 8). Such unipartite teeth however are infrequently produced. Proliferation of the apices of the teeth sometimes occurs (FIG. 13). The proliferations become setigerous or thread-like and attain a length of 20–50 μ. These proliferations remind one of the sporangial ornaments of *Phlyctochytrium chaetiferum* Karling (1), a chytrid which bears several long radiating and branched filaments upon the surface of the sporangium.

The haphazard grouping of the teeth of *P. Aureliae* is in contrast to the remarkable uniformity in the arrangement and number of teeth of the dentigerate species of *Phlyctochytrium*. For example, the sporangia of *P. Zygnematis* (Rosen) Schroeter bear a collarette of four bipartite teeth, and the sporangia of *P. bullatum* Sparrow are ornamented with two concentric whorls of teeth—the inner one composed of four, the outer of two.

Rhizophydium chytriophagum sp. nov.

Zoosporangia epibiotic, eucarpic, spherical, 10–30 μ in diameter, hyaline, smooth-walled, attached to the host by a tubular haustorium 4.2–7.3 μ long, 2.2 μ wide, with short lateral extensions 1.5 μ long. Zoospores spherical, 2.2–2.9 μ in diameter with a single posterior flagellum 15 μ long, and a centrally located refractive globule. Resting spores extramatrical, spherical, 6–15 μ in diameter, wall 1.4 μ thick, golden-brown in color, at germination functioning as a prosporangium.

Zoosporangia epibiotica, eucarpica, sphaerica, 10–30 μ diametro, hyalina, muro tenui, hospiti annexa tubulato haustorio 4.2–7.3 μ longo et 2.2 μ lato et brevibus extentioibus lateralibus 1.5 μ longis praedito. Zoosporae sphae-



FIGS. 14–28. *Rhizophydium chytriophagum.*

ricae, 2.2 μ–2.9 μ diametro, habentes singulum posteriorem flagellum 15 μ longum et globulum refractivum in medio situm. Spora perdurans extramatricalis, sphaerica, 6–15 μ diametro, muro crasso 1.4 μ, colore aureo-fusco. Tempore germinationis spora est pro prosporangio.

Parasitic upon *Phlyctochytrium Aureliae* in a stream at Lake Minnewaska, Ulster County, New York.

The small zoospores of *R. chytriophagum* come in contact with a host sporangium, lose their flagellum and attach themselves to the host by means of a tubular haustorium (FIG. 14). The haustorium is extremely difficult to observe, due to the optical homogeneity of the host's and parasite's cytoplasm. But in those sporangia that are favorably situated or the contents of which are disintegrating the haustorium appears to be a tubular organ 4.2–7.3 μ long and 2.2 μ wide with two short lateral extensions 1.5 μ long (FIG. 17). In most sporangia these details can not be observed and the haustorium, if at all observable, appears to be a simple, short tube (FIG. 20 a). As development proceeds the extramatrical spore cyst increases in size, while its contents become granular and vacuolate (FIG. 20 a). Scattered globules are present that coalesce to form the refringent globules of the zoospore initials (FIGS. 20 b and 21). The changes which take place in the maturing zoosporangia are essentially similar to those previously described for *P. Aureliae*. The sporangia are typically spherical (FIG. 19) and the mature sporangia vary in size from 10 to 30 μ. After cleavage (FIG. 20 c), the zoospores emerge through a rupture in the sporangial wall, forming a quiescent mass at the exit site. The mass soon disperses, the individual zoospores swimming away with the characteristic darting motion of chytrid spores. These zoospores are small, measuring 2.2 2.9 μ in diameter and bearing a single posteriorly attached flagellum 15 μ long (FIG. 22). A single centrally situated refractive globule, 1.2 μ in diameter, is present.

Golden-brown resting spores were readily formed by the parasite and all stages in their development and germination were observed. These spores are spherical and vary from 6 μ in diameter to 15 μ (FIG. 24). The wall is thick, 1.4 μ and smooth. A single, large refractive globule is found in the resting spore, although it may sometimes be surrounded by several smaller ones. A short haustorium similar to the absorbing system of the vegetative zoosporangium comprises the absorbing system of the resting spore (FIG. 24).

The resting spores begin their development in a manner similar to that of the zoosporangia but very shortly the amount of refractive material increases. So much so, that the incipient

resting spores may generally be recognized through the presence of large amounts of refractive material in the cytoplasm (FIG. 23 a). Later stages in development in which the refractive globules have increased considerably in size and number and the wall has begun to thicken are shown in figure 25. With further development the refractive globules coalesce and form a single large one and the wall thickens further as shown in figure 24. As these changes occur the resting sporangium assumes a deep golden-brown color. Sexuality does not appear to be involved in the resting spore formation of *R. chytriophagum.*

Preparations for germination involve a gradual breaking down of the usually single refractive globule and its dispersal throughout the cytoplasm. At this stage a small germ pore is formed in the thick wall of the resting spore and its contents confined in a vesicle emerge through this pore (FIGS. 26 and 27). The vesicle forms the evanescent sporangium where further differentiation of the cytoplasm takes place (FIG. 26). The contents undergo cleavage and the zoospores escape through a rupture in the thin sporangial wall (FIG. 28). These zoospores are similar in size, form and activity to those formed by the vegetative zoosporangia. They, too, are capable of parasitizing sporangia of *Phlyctochytrium Aureliae.*

The literature reveals at least five chytrid hyperparasites that are extramatrical, eucarpic and rhizidiaceous: *Rhizophydium parasitans* Scherffel (**4**), *Phlyctochytrium Synchytrii* Köhler (**2**), *Septosperma anomola* (Couch) Whiffen (**10**), *Septosperma Rhizophidii* Whiffen (**10**), and *Phlyctidium Dangeardii* Serbinow (**6**). The parasite of *Phlyctochytrium Aureliae* is of this nature but differs in many respects from these rhizidiaceous hyperparasites.

Rhizophydium parasitans Scherffel (**4**), which is listed by Sparrow (**9**) among the imperfectly known species of *Rhizophydium*, forms spherical sporangia 8–10 μ in diameter, zoospores measuring 4 μ in diameter with a flagellum 24 μ long and an eccentrically placed refractive globule. *R. chytriophagum* produces sporangia 12–30 μ in diameter, zoospores measuring 2.2–2.9 μ in diameter with a flagellum 15 μ long and a centrally placed refractive globule. The most striking difference between these two species is found in the resting spores. Those of *R. parasitans* are described

as being 6 μ in diameter with a thick, smooth colorless wall. Germination was not observed. The resting spores of *R. chytriophagum*, on the other hand, range in size from 6 15 μ in diameter and are golden-brown in color. Upon germination they function as prosporangia.

The sessile sporangium of *Phlyctochytrium Synchytrii* Köhler (2) is apophysate and bears several exit papillae. *Rhizophydium chytriophagum* forms no definite exit papillae and is non-apophysate. The resting spores of *P. Synchytrii* are colorless and 14 μ in diameter. They, too, function as prosporangia on germination.

The two species of *Septosperma* (10) are quite distinct from *R. chytriophagum* in that their resting spores are bipartite, consisting of an empty basal portion and an apical portion which contains cytoplasm. Germination of these spores was not observed.

Phlyctidium Dangeardii Serbinow (6) is another imperfectly known hyperparasite. Sparrow (9) suggests that it may very well be a species of *Rozella*. Serbinow described it as forming small, ovoid zoospores 1.5 μ long. Dehiscence occurs through a sessile apical pore. The resting spores are thick-walled with an undulating outer wall. Germination was not observed. No rhizoid or haustorium was figured.

From these descriptions it is evident that *Rhizophydium chytriophagum* is to be considered a new species.

SUMMARY—*Rhizophydium chytriophagum* was found parasitizing the sporangia of *Phlyctochytrium Aureliae* collected at Lake Minnewaska, Ulster County, New York. The epibiotic sporangia are spherical and are attached to the host by means of a short, tubular haustorium with two short lateral extensions. Thick-walled, golden-brown resting spores are formed which upon germination act as prosporangia. The parasite has little or no adverse effects upon the host unless more than one parasite attacks the host or if infection occurs early in the host's development.

The host, *Phlyctochytrium Aureliae*, forms sporangia covered with numerous solid, bipartite teeth, arranged in an apparently haphazard order. It is saprophytic, occurring on decaying vegetation and probably on the cast off integuments of insects. It

has been found in New York, New Jersey, Vermont, Virginia and possibly in Denmark.

DEPARTMENT OF BOTANY,
COLUMBIA UNIVERSITY,
NEW YORK 27, NEW YORK

EXPLANATION OF FIGURES

FIGS. 1–13. *Phlyctochytrium Aureliae.* Fig. 1, germinating zoospore; 2, later stage in germination showing branched germ tube; 3, immature sporangium showing development of teeth, apophysis, and rhizoidal system; 4, median optical view of young zoosporangium showing vacuoles and granular cytoplasm; 5 & 6, median optical views of maturing sporangia showing development of teeth and vacuolate cytoplasm; 7, median optical view of older zoosporangium with undifferentiated cytoplasm; 8, surface view of a cluster of bipartite teeth with occasional unipartite teeth; 9, median optical view of mature sporangium with refractive globules; 10, three dimensional surface view of mature zoosporangium; 11, median optical view of sporangium discharging zoospores; 12, zoospore with central refractive globule; 13, proliferation of teeth apices. Fig. 4, × 4,000. Fig. 8, × 1,750. All others, × 3,000.

FIGS. 14–28. *Rhizophydium chytriophagum.* Fig. 14, germ tube of parasite penetrating host; 15, 16 & 18, sporangia of *Phlyctochytrium Aureliae* infected by *Rhizophydium chytriophagum;* 17, median optical view of parasite's haustorium in empty host sporangium; 19, three dimensional view of mature parasite sporangium and host; 20, median optical view of heavily infected host sporangium; 20a, immature vacuolate sporangium of parasite with peg-like haustorium; 20b, refractive globules in cytoplasm of developing parasite sporangium; 20c, parasite sporangium showing cleavage of cytoplasm into zoospore initials; 21, empty host sporangium showing developing parasite sporangium and penetration of haustorium; 22, zoospore of *Rhizophydium chytriophagum;* 23a, incipient resting spore of parasite infecting *Phlyctochytrium Aureliae;* 23b, young parasite; 24, mature resting spore showing thick wall, large refractive globule and forked haustorium; 25, resting spore with several refractive globules developing at the expense of host and second parasite; 26, germinated resting spore showing differentiated secondary sporangium; 27, germination of resting spore with contents emerging in a vesicle; 28, zoospore discharge from evanescent sporangium derived from resting spore. Figs. 14–16, 18, 22, 25 and 28, × 4,000. Figs. 17, 19–21, 23, 24, 26 and 27, × 3,000.

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A NEW DESERT COPRINUS

William H. Long and Vera Menitzer Miller

(with 3 figures)

While on a field trip searching for *Tylostoma*, the senior author discovered a unique agaric herein described as a new *Coprinus*. The outstanding character of the species is the star-shaped remnant of the universal veil which occupies the center of the pileus. Other *Coprini* show veil remnants on the cap, but in no other species examined has there ever been a structure as concrete as there is on this material.

The following description was made from dry material as no fresh plants were available.

Coprinus asterophorus sp. nov.

Sporophoro hypogaeo usque ad maturitatem deinde erumpente. *Pileo* convexo demum subplano, 3–6 cm. lato, reliquiis veli universalis in forma astri conspicuis ornato. *Carne* membranacea. *Lamellis* liberissimis. *Stipite* 5–11 cm. longo, 3–5 mm. crasso, solido deinde cavo. *Annulo* nullo. *Volva* adnata, margine libere angusto. *Sporis* nigris, levibus, ovatis, 14–20 × 10–12.7 μ. *Basidiis* tetrasporis, 29–48 × 10–15 μ.

Sporophore hypogaeous until maturity, then erumpent, originating 2-3 cm. below the surface of the soil, having a well developed universal veil. *Pileus* 3–6 cm. broad, tissue not distinct from that of the stipe, at first obtusely conical expanding to almost plane, with a central sterile disc 6–12 mm. across to which the gills are attached, very young buttons not seen, but ones with gills still white and caps 1.5 cm. broad and 1.2 cm. tall were examined. The expanded pilei have gills connected by an extremely thin, black membrane with fine, light-colored, raised, sandy radial lines or ribs marking the position of the gills on the opposite side. *Cuticle* ripped into fragments by the shrinkage of the volva patch and when the pileus expands, showing as very narrow radiating lines on the naked black context (fig. 1–2) or clinging to the edges of the volval patch in the angles of the arms; in some cases no signs of the cuticle are left on the pileus (fig. 3). Fragments of the cuticle, Tilleul-buff when dry. *Context* membraniform. *Gills* white becoming black, semideliques-

FIG. 1. *Coprinus asterophorus*, mature sporophore showing stellate volva patch and radiating fragments of the cuticle, × 1.

cent, thin, lamellate, radially arranged, close, free, remote from stipe, arcuate at first, then plane, equal throughout, narrow, 1–2 mm. broad (dried), rounded behind, gills of mature specimens connected to one another on the back edge by an onion-skin-thin membrane, on weathering and deliquescing the gills may become free and spread away from each other, twisted, shriveled, giving the frayed appearance one often sees in the older stages of other

Coprini. *Stipe* equal, 5–11 cm long, 3–5 mm. thick, terminating in a bulbous base (FIG 1 & 3), at first white-cottony inside, becoming entirely hollow and consisting only of a tough, thin outer wall, flexible when dry, white at first then buff-colored, exannulate, not woody as in *Montagnites*, exterior not splitting, surface

FIG 2 *Coprinus asterophorus*, expanded pileus, showing radiating fragments of the cuticle, arms of volva patch broken off, × 1 FIG 3. *Coprinus asterophorus*, showing freshly emerged plant with conical unexpanded pileus, no cuticle left, the stellate volva cap was present but fell off from handling × 1

longitudinally appressed fibrillose, with a crinkled undulate appearance when dry. *Bulb* rounded to obtusely pointed, 5–8 mm. broad, solid, entirely sand-covered. *Volva* apparently glutinous before emergence as evidenced by the firmly attached grains of sand, circumscissile, adnate below, with a narrow free limb at top of the bulb, balance of volva remaining on top of pileus as a permanent adhering patch 2–4 cm. broad, soon splitting into 7–10

blunt or acute divisions 6–15 mm. long, the main body of the volva patch covering the disk, but the arms of the star extending halfway to the margin of the pileus, crustose, warted, very sandy, honey-yellow to chamois (Ridgway), easily removable although persistent in the oldest specimens, tissue consisting of closely compacted prosenchyma cells 7.6–12.7 μ broad. *Spores* 14–20 × 10–12.7 μ, ovate to oblong, dark brown under high power (dry), black in mass when viewed with naked eye, smooth, with a large pore at smaller end, minutely apiculate at opposite end. *Basidia* 29–48 × 10–15 μ, clavate, 4-spored. *Cystidia* none. *Trama* of gills narrow, cells rounded.

HABITAT: Solitary or in groups of 2–8 individuals, in open unshaded areas in infertile sandy soil, or in red volcanic soil.

RANGE: Central Arizona, central to southern New Mexico, with a range in altitude from 3400 to 5000 feet.

DISTRIBUTION: New Mexico. Bernalillo County: in an old cow pasture 2 miles south of the Alameda Bridge on the west side of the Rio Grande river, elevation 5000 feet, March 7, 1941, *W. H. Long 9305* (2 plants); 4 miles north of Albuquerque on Highway 85, elevation 5000 feet, June 10, 1941, *W. H. Long 9343* (3 plants); 4 miles north of Albuquerque on Guadalupe Trail on west end of the Denton Addition, June 12, 1941, *W. H. Long 9354* (type) (5 plants); 3 miles north of Albuquerque on Highway 85, June 11, 1940, May 28, 1941, May 24, 1942, *W. H. Long 10427* (1 plant), *9355* (1 plant), *10251* (1 plant). Chavez County: in oak shinnery (*Quercus Harvardii*), 34 miles east of Roswell on Highway 380, elevation 3400 feet, April 19, 1942, *W. H. Long* and *David J. Stouffer 10082* (1 plant). Dona Ana County: 3 miles west of Mesilla Park on Highway 85, elevation 3850 feet, April 19, 1942, *H. L. Barnett 10376* (2 plants in Barnett Herbarium, and 2 plants in Long Herbarium); 5 miles from Las Cruces, elevation 3800 feet, October 1, 1939, *W. H. Long 8434* (2 plants). Arizona. Coconino County: in edge of cinder area, 10 miles east of Flagstaff, elevation 6700 feet, June 16, 1922, *W. H. Long 9106* (8 plants).

Specimens *9305* and *9354* (type) are deposited in the Herbarium of the University of California at Berkeley; all others, unless otherwise stated, are in the Long Herbarium at Albuquerque.

THE TAXONOMIC POSITION OF POLY-POROLETUS SUBLIVIDUS

ROLF SINGER,[1] WALTER H. SNELL [2] AND W. LAWRENCE WHITE [3]

(WITH 4 FIGURES)

In 1934, the second author of this article received from L. R. Hesler a single stipitate sporophore which had certain puzzling features, with a statement that some mycologists to whom it had been submitted could make no satisfactory disposition of it in the Polyporineae, and with the query as to whether or not it could be one of the *Boleti*. The specimen had been collected by A. J. Sharp and J. K. Underwood in pine-oak woods near Allardt, in Fentress County, Tennessee. It was somewhat tough and corky, and had round spores that appeared to be verrucose, and therefore was quite different from anything known in the Boletineae.

In his ignorance of anything of similar nature in the aphyllaphoraceous genera to which it could be referred, Snell (**1936**) described the specimen as a new species and the type of a new genus of Basidiomycetes, with the generic name suggesting the possible relationship to both the polypores and the boletes. Later (**1941**), he placed it in a subgroup, Strobilomyceteae. After a study of the original description, and additional data published by Elrod and Blanchard (**1939**), Singer (**1942**) concluded that the genus *Polyporoletus* belongs in the Aphyllophorales rather than in the Boletineae of the Agaricales.

Recently, White examined the specimen and was immediately struck with its resemblance to *Scutiger caeruleoporus* (Peck) Murr., with which he is familiar. A careful anatomical analysis of the type of *Polyporoletus sublividus* and comparison with the available specimens of the *Scutiger caeruleoporus* group, carried

[1] Harvard University.
[2] Brown University.
[3] Philadelphia Tropical Deterioration Research Laboratory, formerly Harvard University.

out by Singer and White, convinced us of the generic identity of *Polyporoletus* and *Scutiger*. Further, it was noted that *S. retipes* (Underwood) Murr. is so similar to *P. sublividus* as to suggest specific identity. Since the spores of the type specimen of *S. retipes*, however, are found to measure 8.5–9 × 5.3–6.8 μ and to have a simple, thin, entire and smooth wall, they differ from those of *P. sublividus*, as will be noted below.

The reasons for the proposed transfer of *P. sublividus* from the boletes to *Scutiger* are the following:

(1) No trace of a bilateral trama in the pore walls of *P. sublividus* is found in sections of the hymenophore. This observation agrees with indications of Elrod and Blanchard.

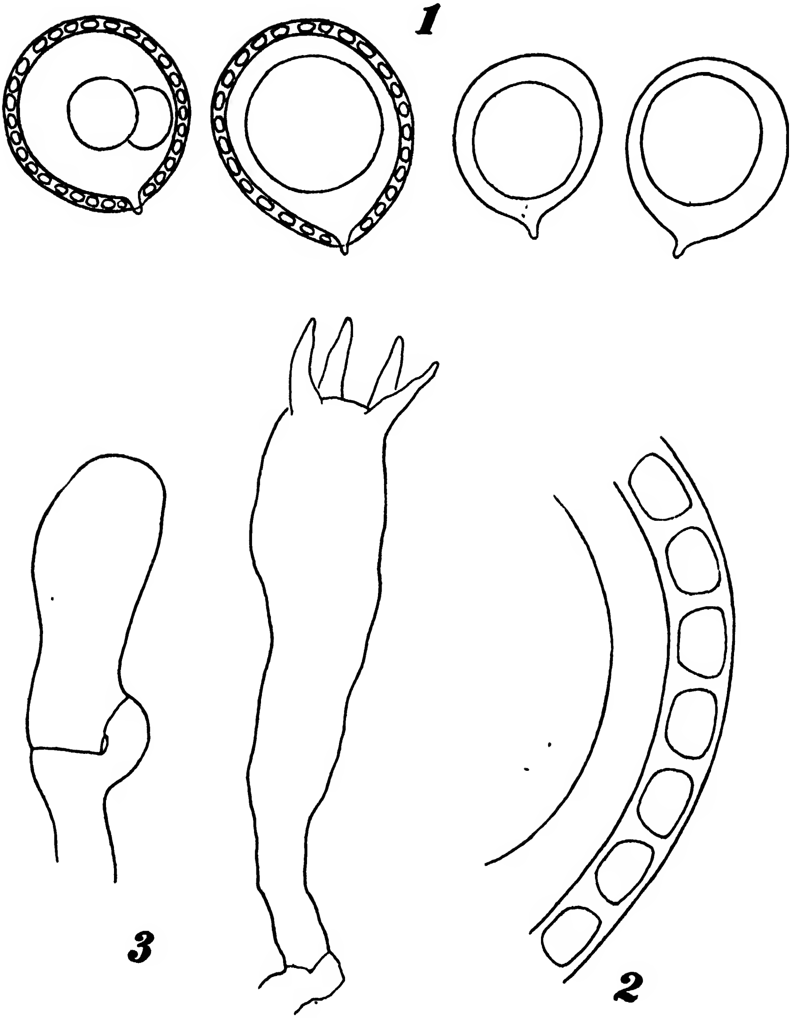
(2) Numerous clamp connections are present on the septa of the hyphae of *P. sublividus*. This is often the case in *Scutiger*, but never in the Strobilomycetaceae. Only *Gyrodon*, *Paragyrodon*, *Gyroporus* and *Phaeogyroporus*, and some species of *Boletinus* and *Phylloporus* have clamp connections, but in these genera all the other anatomical characters are in disagreement.

(3) The spores of *P. sublividus* are definitely hyaline under the microscope. Hyaline spores are not known in the Strobilomycetaceae and rarely occur in the Boletaceae (genus *Tylopilus*). In this latter genus, the species concerned are of an entirely different type as compared with *Polyporoletus*. A white spore print which *Polyporoletus* would be expected to produce, does not occur in the Boletineae.

(4) There are no cystidia nor cheilocystidia present in *P. sublividus*. The sterile bodies that can be found are best described as cystidioles. This situation does not agree with that known in the Strobilomycetaceae or Boletaceae.

One puzzling problem remains. Snell (l.c.) indicated that the spores of *Polyporoletus sublividus* are verrucose. No rough spored *Scutiger* is known. Reexaminations of the spore-wall of the specimens in question in all kinds of mounting media with a high-power oil-immersion objective by Singer and White did not furnish a clear understanding of the structure of the wall. The spores appeared to be rough because of an incrustation which disappeared more or less completely in alkaline solutions. With this treatment, some of the spores were perfectly smooth and

1



FIGS. 1–3. *Scutiger sublividus.*

thin-walled, differing from the spores of *Scutiger retipes* only in the measurements (8–9.5 × 6.3–7.7 μ) while others still appeared indefinitely rough or spinose. Since the spores are non-amyloid, Melzer's reagent did not improve the optical differentiation of the wall.

In previous studies on the anatomy of *Favolaschia*, Singer had used brilliant cresyl-blue as a very satisfactory dye for basidio-

mycetous tissues. When using this dye after a short treatment with KOH in order to dissolve the incrustation, and after having replaced the alkali by water, he obtained a slight violet coloration of the walls. If, for a double-staining effect, the cell-sap is

Fig. 4 *Scutiger sublividus*

colored pinkish-red by phloxine, the structure of the seemingly rough walled spores becomes distinct. It now appears that the spores are not rough at all, but that the wall has a lacunose-cellular structure. There are actually two thin walls between which there are radially connecting walls forming loculi. These loculi included by the two walls and the radial connections have liquid contents. With the double stain, the loculi appear pink

as stained by the phloxine, while the separating walls are stained pale violet by the cresyl-blue. When the upper surface of the spores is focused upon, the loculi appear as lighter shining spots. We did not succeed in proving that there is no connection between the loculi and the part of the spore inside the inner wall; in other words, it is still possible that the inner wall is minutely perforated. On the other hand, the existence of smooth spores with thin and simple or double wall in the same preparation suggests that the inner wall or at least the connecting vertical walls are of a secondary character, formed at full maturity only.

This strange structure is entirely new for basidiomycetous spores, and as far as we know, for fungus spores in general. We propose the term "lacunose spore-wall" for a wall structure of this kind.

The close relationship between *S. retipes* and *P. sublividus* makes it impossible to base a genus *Polyporoletus* on the only character distinguishing the latter from *Scutiger*—*i.e.* the lacunose spore-wall—inasmuch as spores with normal (simple and homogenous) spore wall, not differing from this of *Scutiger*, are always found in the preparations of *Polyporoletus sublividus*. It would therefore appear that this latter species must be called **Scutiger sublividus** (Snell) Singer, Snell & White, comb. nov.

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EXPLANATION OF FIGURES

FIGS. 1–4. *Scutiger sublividus* (Snell) Sing., Snell & White. 1, spores, × 3000. Del. W. L. White. 2, part of the spore walls, the line at their left side indicating the position of the central oil drop; greatly enlarged. Del. W. L. White. 3, basidiole and basidium, × 540. Del. W. L. White. 4, dried carpophore in natural size. Phot. Walter H. Snell.

ACTINOPELTE DRYINA

Donald P. Limber [1] and Edith K. Cash [2]

Several collections of a fungus associated with leaf spots of oak and other deciduous trees have recently come to the attention of the writers. These include a leaf spot on *Liquidambar styraciflua* from Monmouth County, N. J.,[3] two collections on *Quercus rubra* from Morris Plains, N. J., a collection on *Quercus nigra* from Richmond Hill, Ga., and a specimen on *Eucalyptus* sp. from Avery Island, La. The fungus in each instance appears to be identical with *Leptothyrium dryinum* Sacc., a well-known species distributed in Europe and North America, but apparently hitherto reported only on *Quercus*. Exsiccati specimens and numerous other collections of this species from various sources have been studied and have revealed unreported features of its morphology. From an examination of the literature it is apparent that in none of the published accounts of *L. dryinum* has an accurate and complete description been given of its structure, particularly with reference to the attachment of the fruiting body to the leaf surface of the host.

Leptothyrium dryinum Sacc. was described in 1878 (**11**, p. 202) as occurring on leaves of *Quercus pedunculata* in northern Italy, the specimen cited having been issued in 1876 as Mycotheca Veneta no. 555 under the name of "? *Stigmella dryina* Lév." Other collections of the species have been made in Europe and North America on various species of *Quercus*, and there are numerous references in the literature to its occurrence. Neither

[1] Plant Quarantine Inspector, Division of Foreign Plant Quarantine, Bureau of Entomology and Plant Quarantine, Agricultural Research Administration, U. S. Department of Agriculture.

[2] Associate Mycologist, Division of Mycology and Disease Survey, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.

[3] These specimens were taken by inspectors of the U. S. Department of Agriculture Bureau of Entomology and Plant Quarantine in the Special Survey made of the areas in the vicinity of the maritime ports in 1943–1944.

the brief original description nor any other early reference to the species establishes the fact that it differs from the Leptostromataceae, as interpreted by modern authors, in that the fructifications are not innate but superficial, and the sporulation inverse, that is, the conidia are borne on the under side of a scutellum, which is attached to the leaf by a central columella. Bubák and Kabát (**2**, p. 44) commented on the superficial character of the fruiting bodies but gave no detailed account of their structure. The species was redescribed by von Hoehnel in 1925 (**8**, p. 69) under the name *Actinopelte dryina* (Sacc.) Hoehn. and assigned to his previously established family Actinothyriaceae. Von Hoehnel restricted the application of the name *A. dryina* to European collections of the fungus and erected the new species *A. americana* for the American specimen which he had examined.

The genus *Actinopelte* was established by Saccardo in 1913 (**12**, p. 315), the type being *A. japonica* Sacc., found on leaves of *Castanea vesca* var. *japonica* from Japan. The fungus was considered by Saccardo to be an ascomycete, and the large subglobose bodies underneath the scutellum were thought to be monosporous asci. Later in the same year Theissen (**17**, pp. 507–508, *f. 6*) pointed out that these so-called asci are really conidia and described the manner in which they are borne. His figure shows the radiating strands of the scutellum and the attachment of the conidiophores to its lower surface close to the central columella. Theissen's view was later confirmed by Petrak (**10**). In both Theissen's description of *A. japonica* and von Hoehnel's account of *A. dryina* and *A. americana* the central columella was erroneously described as composed of small-celled pseudoparenchyma. This interpretation is not borne out by an examination of the available specimens, including exsiccati cited as representing the three species. No such pseudoparenchymatous tissue was seen, the scutellum being in every case connected to mycelium within the host tissues by a large, hyaline, central cell. This type of structure is apparently the same as that noted by Tehon and Stout (**16**, p. 192, *f. 7*) in their description of *Leptothyrella Liquidambaris* and in the discussion by Tehon (**15**) of his proposed family Rhizothyriaceae.

Examination of herbarium specimens and a study of the literature have brought to light additional records of *L. dryinum* on various hosts and under several specific names. It is quite probable that others have been overlooked and may be added to the synonymy later.

Leptothyrium castanicolum Ellis & Ev. was collected by Ellis on *Castanea vesca* in New Jersey and issued as North American Fungi no. *3168* and as Fungi Columbiani no. *782*. These specimens have the same data and the material shows evidence of being from a single collection. The label of N. Am. Fungi *3168* bears the note "Very near *L. dryinum* Sacc.," and that of the Fungi Columbiani specimen "Perhaps too near *L. dryinum* Sacc.," indicating that Ellis recognized the close similarity of his species to that of Saccardo. The brief original description gives no spore measurements, but an examination of the exsiccati specimens cited proves that in this, as in other characters, the species on *Castanea* is not specifically distinct from *L. dryinum*.

Two specimens in the Ellis Collection in the New York Botanical Garden, one on apple leaf labeled as *Leptothyrium dryinum* Sacc. f. *Mali* Ellis & Ev., the other on *Sassafras officinale* as *L. dryinum* Sacc. f. *Sassafras*, also proved on examination to be the same as the species on *Quercus*. The forms "mali" and "sassafras" are presumably unpublished herbarium names.

Actinopelte americana Hoehn. is based on an Ellis collection on *Quercus coccinea* from New Jersey issued as Fungi Columbiani no. *286*. The description of this species is nearly identical with that of *A. dryina* (Sacc.) Hoehn. in the same article (**8**). The spores are said to be hyaline and 10-12 $\times$ 6–7 μ in *A. americana*, subhyaline and 12-14 $\times$ 7–8 μ in *A. dryina*. This slight difference in dimensions is no greater than the variation that could reasonably be expected within a species, and the color of the spores also ranges from hyaline to yellowish or pale brown with age and condition of the specimens. In recording the fungus from Iowa, Gilman and Archer (**4**, p. 306) have therefore reduced *A. americana* to synonymy.

A report of *Actinopelte japonica* Sacc. on several species of *Quercus* (black, chestnut, and red oaks) from New Jersey was

made in 1914 by Schwarze (**13**). It is most probable that the fungus concerned was *A. dryina* rather than *A. japonica*, since the spore dimensions given (5–7.7 × 10–15 μ) agree with those in the former, rather than the Japanese species. According to Theissen, the spores of *A. japonica* are 50–60 × 40–48 μ; in the exsiccati specimen examined, Sydow Fungi Exotici exsiccati no. *526* on *Castanea pubinervis* from Japan, they were found to measure 30–48 × 28–37 μ.

Actinopelte japonica has also been listed by Archer (**1**, p. 361) from West Virginia on *Quercus marilandica*, *Q. prinus*, and *Quercus* sp. The specimens cited (nos. *3207*, *3218*, and *3350*) have been examined and prove to be unquestionably *A. dryina*.

Other possible synonyms of *Actinopelte dryina* include three species described from Illinois: *Leptothyrella* (as "*Leptothyriella*") *Liquidambaris* Tehon & Stout (**16**, p. 192, *f. 7*) on *Liquidambar styraciflua*, *Pirostoma Nyssae* Tehon (**14**, p. 137, *f. 7–8*) on *Nyssa sylvatica*, and *Actinothyrium gloeosporioides* Tehon (**14**, p. 136, *f. 3–6*) on *Sassafras variifolium*. Type material of these species has not been examined. The spores of *Pirostoma Nyssae* are said to be olivaceous to brown and slightly verrucose. While brownish spores are frequently found in *A. dryina*, they are, however, smooth, so far as has been observed. Verrucose spores, if the normal condition in *P. Nyssae*, would therefore preclude its being considered synonymous with *A. dryina*. It should be noted that neither *Leptothyrella* nor *Pirostoma* is a valid generic name, as pointed out by Diedicke (**3**, p. 174) for the former and by von Hoehnel (**5**) for the latter. Since the spores in *Actinothyrium graminis* G. Kunze, the type of the genus, are acicular, *Actinothyrium gloeosporioides* would seem to be closer to *Actinopelte* than to the genus in which it was described.

Unless some earlier synonym should be discovered, von Hoehnel's name *Actinopelte dryina* appears to be the valid name for the species. Because of the incomplete or erroneous data given in various accounts of this fungus, it seems advisable to give the following emended description, based on examination of recent collections and numerous herbarium specimens.

ACTINOPELTE DRYINA (Sacc.) Hoehn. Mitt. Bot. Inst. Tech. Hochsch. Wien **2**: 69. 1925.

Leptothyrium dryinum Sacc. Michelia **2**: 202. 1878.

Leptothyrium castanicolum Ellis & Ev. Jour. Myc. **4**: 103. 1888.

Actinopelte americana Hoehn. Mitt. Bot. Inst. Tech. Hochsch. Wien **2**: 68. 1925.

Actinopelte japonica Auct. Amer., nec Sacc.

Leptothyrium dryinum Sacc. f. *mali* Ellis & Ev. ined. (Ellis Coll. in New York Botanical Garden).

Leptothyrium dryinum Sacc. f. *sassafras* Ellis & Ev. ined. (Ellis Coll. in New York Botanical Garden).

?*Actinothyrium gloeosporioides* Tehon, Mycologia **16**: 136. *pl. 13, f. 3-6.* 1924.

?*Pirostoma Nyssae* Tehon, Mycologia **16**: 137. *pl. 13, f. 7-8.* 1924.

?*Leptothyrella Liquidambaris* Tehon & Stout, Mycologia **21**: 192. *pl. 13, f. 7.* 1929.

Spots small, suborbicular, brownish or reddish brown, margin definite, 2–5 mm. in diam. (the fungus sometimes found on large irregular spots, but then probably as a secondary invader); fructifications superficial, numerous, unevenly scattered, usually epiphyllous, rarely hypophyllous, 60–110 μ in diameter $\times$ 20–40 μ thick, mostly 70–90 $\times$ 20–30 μ; scutellum membranous, suborbicular, slightly to strongly arched, umbilicate at the center, surface ribbed, central cell hyaline or subhyaline, 7–8 μ in diameter, membrane of yellowish- or greenish-brown, septate, 1–3 bifurcate, hyphal strands radiating to the margin, hyphal ends free as blunt or sharp-pointed spines up to 15 μ long, scutellum borne on a stalk or columella; columella a single cell, subhyaline, oblong with rounded or truncate ends, 10–34 $\times$ 5–9 μ, mostly 17–25 $\times$ 7–8 μ, connected to the mycelium within the leaf by a slender strand at the base; fertile tissue of small, parenchymatous, hyaline to subhyaline cells surrounding the upper part of the columella, arising from the under side of the scutellum near the central cell and bearing the conidiophores which extend downward and outward forming a loose sheath about the columella; conidiophores from short, nearly papillate, up to 12 μ long, straight or curved, swollen at the base, then tapering to a slender neck about 1 μ wide; conidia acrogenous, broad elliptic to subglobose, with rounded ends or the base rarely acute, double

walled, hyaline to pale olivaceous, 10–14 × 6–9 μ, mostly 11–12.5 × 7–8 μ, pushed out from beneath the outer edge of the scutellum when mature.

Hab. in living leaves of *Quercus* spp. and other broadleafed trees in North America and Europe.

Specimens examined:[4] on *Castanea vesca*, New Jersey, 1894, Ell. & Ev. Am. Fungi *3168* and F. Col. *782*, and Mississippi, 1921, E. K. Bynum; *Eucalyptus* sp., Louisiana, 1944, L. A. Mayer *805* (S. S. B. E. P. Q.); *Liquidambar styraciflua*, Maryland, 1913, C. L. Shear (Myc. Coll.), and New Jersey, 1943, E. Kostal *50* (S. S. B. E. P. Q.); *Nyssa sylvatica*, Virginia, 1922, W. W. Diehl; *Pyrus malus*, New Jersey, 1888, J. B. Ellis (N. Y. Bot. Gard.); *Quercus borealis* (?), New York, 1939, Dept. Pl. Path. Cornell Univ. *28869; Q. coccinea*, New Jersey, 1881, Ell. N. Am. Fungi *732* and F. Col. *286* (Myc. Coll.), Ellis Coll. *2492* (N. Y. Bot. Gard.), and Iowa, 1913, J. P. Anderson; *Q. marilandica*, West Virginia, 1928, W. A. Archer *3207; Q. nigra*, Georgia, 1943, A. W. Blizzard *809* (S. S. B. E. P. Q.); *Quercus palustris*, Virginia, 1905, G. W. Koiner; *Q. pedunculata, Type*, Italy, Sacc. Myc. Ven. *555; Q. phellos* (?), South Carolina, 1930, G. A. Meckstroth; *Q. prinus*, West Virginia, W. A. Archer *3212; Q. pseudorubra*, Italy, Thuem. Myc. Univ. *1584; Q. rubra*, New Jersey, 1943, M. A. McMaster, Limber *17* (S. S. B. E. P. Q.), and West Virginia, 1896, L. W. Nuttall; *Q. stellata*, Mississippi, 1922, L. E. Miles *752; Q. velutina*, Wisconsin, 1921, 1925, 1927, 1931, J. J. Davis; *Quercus* sp., Virginia, 1924, J. R. Winston, and 1929, R. W. Davidson *2048-A;* West Virginia, 1928, W. A. Archer *3218* and *3350;* Kansas, 1922, R. W. Davidson; Texas, 1915, G. L. Fisher; *Sassafras officinale*, New Jersey, 1894, J. B. Ellis (N. Y. Bot. Gard.).

In old, stained, permanent mounts an appearance of septation in the columella can sometimes be observed. Whether this is merely simulation due to unequal staining of the cell contents, or whether a few septa develop with age is not certain. In the

[4] Unless otherwise stated, specimens cited are in the Mycological Collections, U. S. Bureau of Plant Industry Station, Beltsville, Md. Collections from the Special Survey, Bureau of Entomology and Plant Quarantine, are designated as S. S. B. E. P. Q.

few instances in which this condition has been observed the apparent divisions of the columella were large. The color of the scutellum is quite constant in a given collection but varies from light olivaceous to dark green or greenish brown in different collections, even in the same host genus, as *Quercus*. As the fungus matures under conditions favoring abundant production of conidia, the strands of the scutellum tend to separate, presumably from the pressure of the mass of conidia beneath, so that the texture appears looser, and the scutellum sometimes becomes almost completely disintegrated.

The classification of *Actinopelte* is difficult to determine; its relationship to macroscopically similar genera is uncertain, owing principally to a lack of data on the details of their structure. In his emended description of the genus, Theissen gave no indication as to the family of which he considered it a member. Naoumoff (**9**, p. 428) suggested including *Actinopelte* with his new genus *Rhizothyrium* in the Pycnothyriaceae. In his System der Fungi Imperfecti (**6**, pp. 310, 353), von Hoehnel erected the family Actinothyriaceae to include *Actinothyrium* G. Kunze and *Actinopelte* Sacc., adding a third genus, *Columnothyrium* Bubak, to the family two years later (**7**). The characters by which it may be distinguished from the Pycnothyriaceae are not clearly stated, the presence or absence of a superficial mycelium or subiculum not being mentioned. Although both families are characterized by radiate scutella and inverse sporulation, the Pycnothyriaceae are placed as pycnidial forms near the Leptostromataceaë in von Hoehnel's key, while the Actinothyriaceae are classed with the Tuberculariaceae on the basis of being devoid of true pycnidia. A new family, Actinopeltaceae, having the characters of its single genus *Actinopelte*, was proposed a year later by Petrak (**10**), without reference to von Hoehnel's classification.

More recently the family Rhizothyriaceae has been erected by Tehon (**15**) to include forms with superficial, radiate fructifications which have inverse sporulation as in the Pycnothyriaceae, but which differ from that family in being devoid of superficial mycelium and in the attachment of the fruiting body, here named "rhizothyrium," by a columella to mycelium within the host

tissue. This family, like Petrak's Actinopeltaceae, does not appear to differ from von Hoehnel's Actinothyriaceae, but is clearly defined. *Rhizothyrium* Naum. and *Actinothyrium* G. Kunze are included by Tehon in the Rhizothyriaceae, but *Actinopelte* is not listed.

A knowledge of the ascus stage of *Actinopelte*, as yet not established, would undoubtedly aid materially in determining the taxonomic position of the genus. Von Hoehnel (7) refers to the Actinothyriaceae as "Nebenfruchtformen, vielleicht von Microthyriaceen"; this does not help to distinguish them from the Pycnothyriaceae, which he had definitely stated to be pycnidial forms of the Microthyriaceae. A possible connection with *Dasyscypha* or *Lachnum* was later suggested by von Hoehnel (8) for *Actinopelte dryina*, but no evidence is given for this assumption. According to Tehon (15) the morphology of the Rhizothyriaceae suggests that they may be pycnidial forms of the Polystomellaceae.

It is obvious that further data obtained from a more detailed study of these fungi will be necessary before any satisfactory classification can be attempted. On the basis of present knowledge, Tehon's grouping of the Rhizothyriaceae (= Actinothyriaceae Hoehn.) with the Pycnothyriaceae in a proposed order named the Pycnothyriales appears more logical than von Hoehnel's classification, in recognizing both the differences between these two families and the common characters that distinguish them from the Leptostromataceae.

The writers are indebted to Dr. F. J. Seaver of the New York Botanical Garden and Dr. D. H. Linder of the Farlow Herbarium for the privilege of examining herbarium specimens in connection with this study.

U. S. BUR. ENTOMOLOGY AND PLANT QUARANTINE,
HOBOKEN, N. J.
U. S. PLANT INDUSTRY STATION,
BELTSVILLE, MD.

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FABRIC DETERIORATION BY THIRTEEN DESCRIBED AND THREE NEW SPECIES OF CHAETOMIUM[1]

GLENN A. GREATHOUSE[2] AND L. M. AMES[3]

(WITH 7 FIGURES)

The rapid deterioration of military fabrics in many tropical and subtropical areas has focused attention on cellulose decomposing microorganisms, prominent among them being species of the genus *Chaetomium*. Species of *Chaetomium* have been listed among the cellulose destroyers for many years; however, the information being largely observational (**26**, **14**, **27**). Few studies have been carried out to determine the importance of species other than *C. globosum* Kunze in the deterioration of cellulose materials. Frequently other species of *Chaetomium*, such as *C. elatum*, *C. funicolum* have been isolated from cotton fabrics. Approximately one-half of the known species of *Chaetomium* are included in this study.

In many early studies on deterioration of cellulose by microorganisms, true distinction was not made between decomposition of cellulose and other carbohydrates. In other words, if an organism was observed to grow on wood or stubble, it was classified as a cellulose decomposer. Such organisms may utilize carbon sources other than cellulose. Greathouse, Klemme, and Barker (**15**) developed a method that offers advantages in evaluating the ability of microorganisms to digest high-polymer cellulose. The evidence included in the present paper establishes more certainly the ability of sixteen species of *Chaetomium* to decompose cotton fabric under varied conditions through the use

[1] Grateful acknowledgment is made to Katharina Bollenbacher for aiding with the transfer of cultures and breaking strength measurements.

[2] Formerly Physiologist, Bureau of Plant Industry, Soils and Agricultural Engineering, U. S. Department of Agriculture. Now Director of the Information Center, Joint Army-Navy-NDRC, Tropical Deterioration Project.

[3] Pathologist, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture.

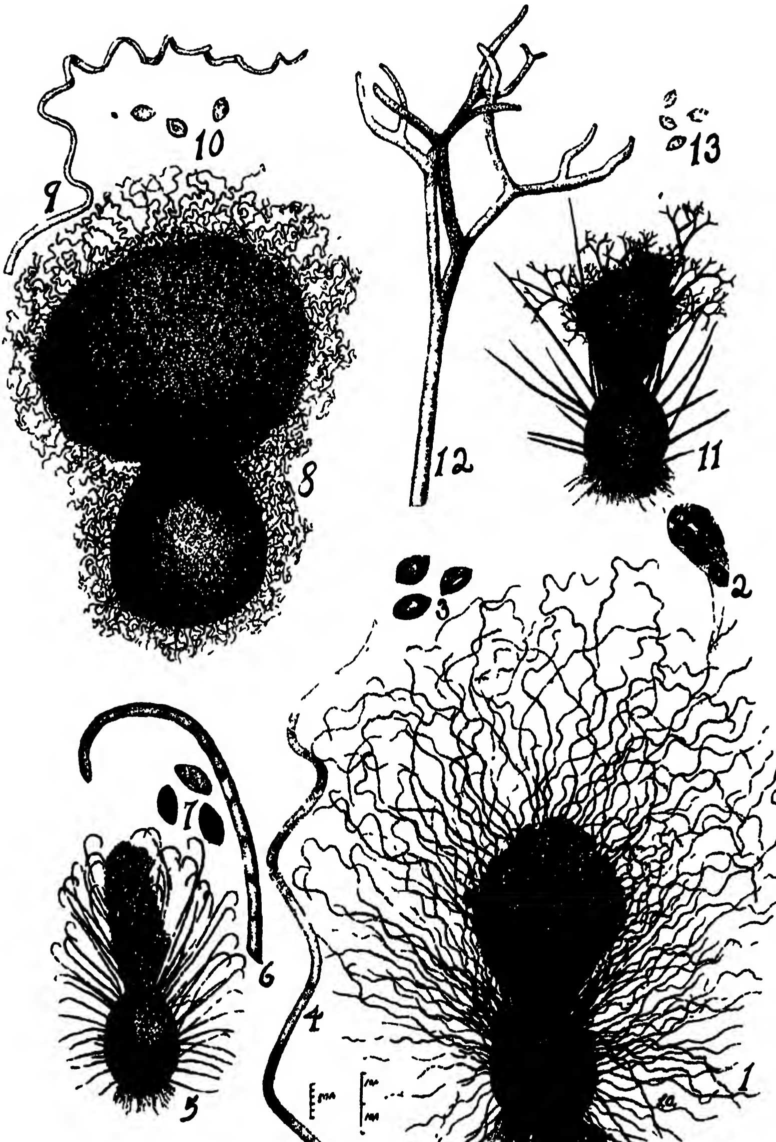

FIG. 1. 1–4, *Chaetomium globosum* Kunze, 1, mature perithecium; 2, ascus containing ascospores; 3, mature ascospores; 4, terminal hair; 5–7, *Chaetomium aureum* Chivers; 5, mature perithecium; 6, terminal hair; 7, mature ascospores; 8–10, *Chaetomium ochraceum* Tschudy; 8, mature perithecium; 9, terminal hair; 10, mature ascospores; 11–13, *Chaetomium funicolum* Cooke; 11, mature perithecium; 12, terminal hair; 13, mature ascospores.

of this method. Drawings of the *Chaetomium* species are included to aid readers to visualize the organisms herein described.

LITERATURE REVIEW

In 1817 Kunze (**17**) published a description of a hitherto unrecognized genus giving to it the name *Chaetomium* and described the first species under the name *C. globosum*. One year later he published a description of a second species which he called *C. elatum* (**18**). Corda (**7, 8, 9**) amended the original description given by Kunze and described two new species that are still accepted, *C. indicum* and *C. murorum*. Fuckel (**12**) and Cooke (**6**) also made valuable contributions in their descriptions of two new species under the names *C. crispatum* and *C. funicolum*.

Zopf (**30**) described as new *C. spirale* and described or redescribed *C. cuniculorum* and *C. bostrychodes*. *C. contortum* was described by Peck (**24**) in 1896 and *C. simile* by Massee and Salmon (**21**) in 1902. Palliser (**23**) described for the first time *C. aterrimum* under a name given it by Ellis and Everhart (**11**). She also described the species *C. cochliodes*, *C. spirochaete*, and *C. flexuosum* as new. Tschudy (**29**) described two new species, *C. ochraceum* and *C. cancroideum*, which were isolated from decomposing reeds.

Bainier (**2**) published a monograph of the genus *Chaetomium* in the year 1910. He gave a brief historical sketch and a review of the genus. In addition, Bainier described 22 species and 3 varieties, 12 species and 2 varieties of which are described under new names; in this work the synonymy of the genus was increased.

In 1910 Palliser published a revision of the *Chaetomiaceae* in the North American Flora, where 17 species are enumerated including descriptions on three species previously unknown.

Chivers (**10**) gives the characteristics of the genus *Chaetomium* and a key to 28 species in an outstanding monograph.

Unidentified Chaetomia have been isolated from cotton fabrics under many different conditions and locations (**4, 5, 14, 19, 22, 26**). In 1934 *Chaetomium globosum* was selected by Thom et al (**27**) as a suitable test organism for evaluating the mildew resistance of outdoor cotton fabrics. This fungus has since been employed in many Government and Commercial laboratories in

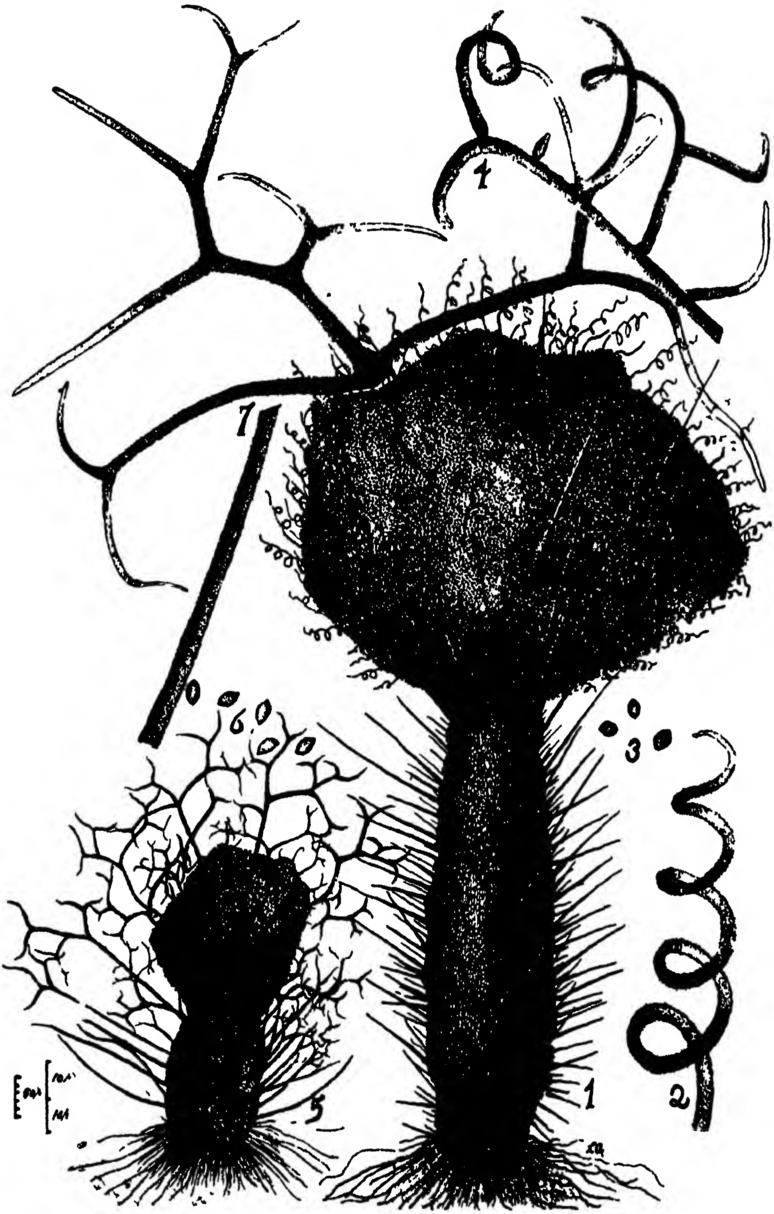

FIG. 2. 1–3, *Chaetomium caprinum* Bainier; 1, mature perithecium; 2, 4, terminal hairs; 3, mature ascospores; 5–7, *Chaetomium elatum* Kunze & Schmidt; 5, mature perithecium; 6, mature ascospores; 7, terminal hair.

connection with the evaluation of mildew-preventives applied to fabrics (**3**, **13**, **15**, **16**, **20**, **25**). Thom et al (**27**) states: "It has thus been shown that *Chaetomium* is a common cause of destruction of awnings, paulins, bags, shock covers, and tentage in the field."

MATERIAL AND METHODS

Bleached, 8-ounce Army duck, with an original breaking strength of 140.5 lbs., was used throughout these investigations. Before exposure to the attack of fungi, the fabric was treated to remove sizing finishes, any residual waxes, pectins, and other substances that might serve as added nutrients. For the degreasing procedure the fabric was extracted twice for 2 hours each in two changes of carbon tetrachloride, followed by a treatment with 0.05 per cent starch and protein-solubilizing enzyme and thoroughly rinsed in distilled water (**1**).

The fabric was divided into large blocks so that each block would furnish one of the ten replicates used for each determination. The blocks were cut into strips measuring 15 cm. (6 inches) in the warp direction by 3.1 cm. (1.25 inches) and by raveling the width was reduced to exactly 2.5 cm. (1 inch) (**1**).

The "glass-wick" procedure and the nutrient medium designated as Formula A [4] described by Greathouse, Klemme and Barker (**15**) was used. The inoculated strips of fabric were incubated for a 7-day period in a darkened, air conditioned room which was maintained at 85° to 86° F. (29.4 to 30° C.) and 90 to 94 per cent relative humidity. Other experiments have shown that this is approximately the optimum temperature for *C. globosum* to yield the greatest loss in breaking strength of cotton fabric. All results are based on the average change of tensile strength of ten strips subjected to individual isolates.

The final strength of the test fabric after incubation with the fungus was recorded in pounds and calculated as the percentage of the original breaking strength.

The pH values of the media were determined with the aid of the Beckman glass-electrode apparatus.

[4] K_2HPO_4 1.3940 g., $MgSO_4.7H_2O$ 0.7395 g., NH_4NO_3 1.0006 g., Fe, Zn and Mn 0.001 g. per liter distilled water.

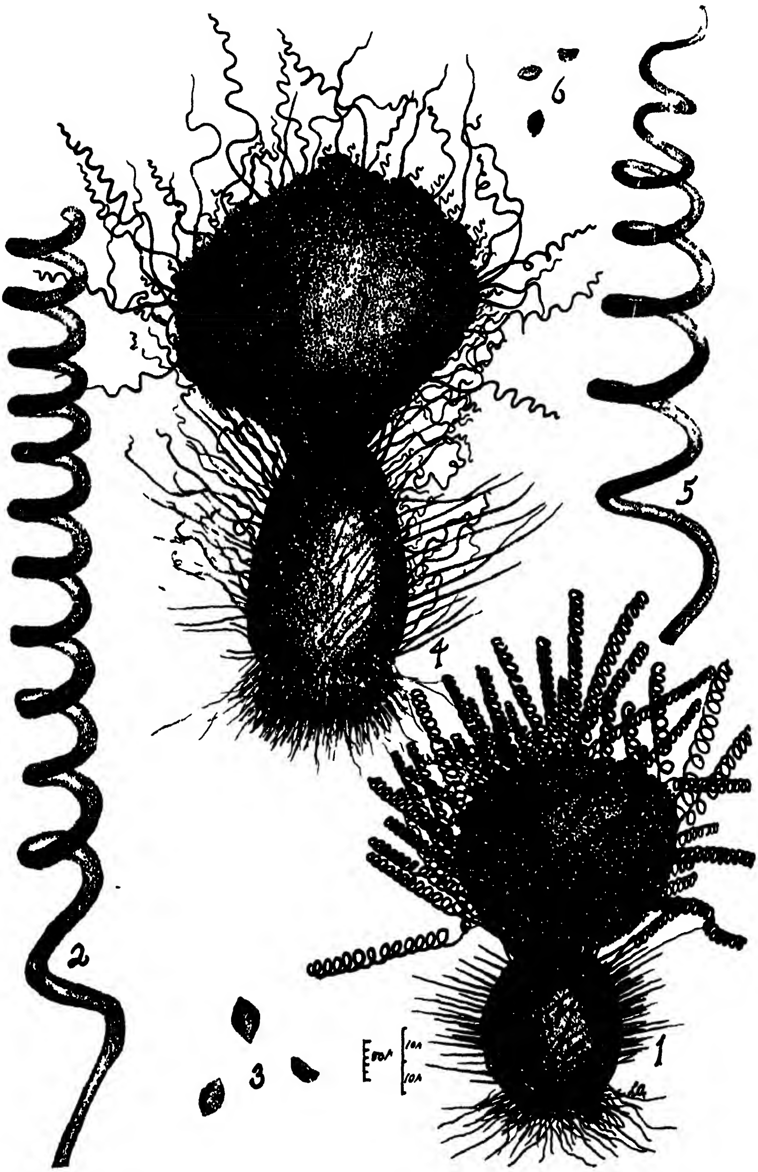

FIG 3. 1–3, *Chaetomium aterrimum* Ellis & Ev., 1, mature perithecium, 2, terminal hair, 3, mature ascospores, 4–6, *Chaetomium cochliodes* Palliser, 4, mature perithecium, 5, terminal hair, 6, mature ascospores.

Four isolates of *C. globosum* Kunze, two isolates each of *C. funicolum* Cooke, *C. elatum* Kunze & Schmidt, and *C. cochliodes* Palliser, and one isolate each of *C. caprinum* Bainier, *C. ochraceum* Tschudy, and a second species described as *C. cancroideum* Tschudy, which morphologically resembles *C. funicolum*, *C. aterrimum* Ellis & Ev., *C. aureum* Chivers, *C. murorum* Corda, *C. contortum* Peck, *C. bostrychodes* Zopf, *C. convolutum* Chivers, *C. dolichotrichum* Ames, *C. microcephalum* Ames, *C. pachypodioides* Ames, were used in this investigation. These fungi were cultured on the cotton fabric in contact with the mineral salts medium described as Formula A and on three subsequent media modified only by the substitution of equivalent amounts of nitrogen in the form of $NaNO_3$, $(NH_4)_2SO_4$, and $NH_4H_2PO_4$. The nitrogen content of these media is 0.350 gram per liter. The original pH values of these media were 7.1, 6.6, 5.8, and 5.5 respectively. After the growth of *Chaetomium* species the pH range was 6.7–8.4, 5.8–6.6, 4.6–5.8, and 4.3–5.5, respectively.

TABLE I

THE SOURCE AND IDENTIFICATION OF CHAETOMIUM ISOLATES USED IN THIS INVESTIGATION

Species	Isolate number	Source and location of isolate	Identified by:
C. globosum	1042.4	Collection of Chas. Thom	A. H. Chivers
C. globosum	1042.5	G. W. Martin—1410, Barre Colorado Isl., Aug. 1937	L. M. Ames
C. globosum	1042.6	G. W. Martin—4312, Panama, Prov. Chirique, alt. 2000 m., Aug. 1937	L. M. Ames
C. globosum	1042.7	Mycologists—Australia	L. M. Ames
C. caprinum	1043.0	L. M. Ames from New England	L. M. Ames
C. cancroideum	1044.4	Tschudy—decomposing reeds, State of Washington	R. H. Tschudy
C. funicolum	1043.1	Warehouse cotton—K. Bollenbacher	L. M. Ames
C. funicolum	1043.2	L. M. Ames—from the Great Smoky Mts. of Tennessee	L. M. Ames
C. elatum	1043.4	H. Humfeld—storage cotton	L. M. Ames
C. elatum	1043.5	K. Bollenbacher—Mattress cotton	L. M. Ames
C. cochliodes	1043.6	G. W. Martin—3855, B. Columbia, Sierra Nevada de Santa Marta, alt. 1250 m., August 1935	L. M. Ames
C. cochliodes	1043.7	G. W. Martin—4558, Panama Canal Zone, Summit, August 1937	L. M. Ames
C. ochraceum	1044.5	Tschudy, decomposing reeds, State of Washington	R. H. Tschudy
C. aterrimum	1043.8	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. aureum	1043.9	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. pachypodioides	1044.3	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. convolutum	1044.0	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. murorum	1044.8	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. contortum	1044.9	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. microcephalum	1045.0	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. dolichotrichum	1044.7	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames
C. bostrychodes	1045.1	L. M. Ames from the Gr. Smoky Mts.	L. M. Ames

The source and identification of the *Chaetomium* species used in this investigation are recorded in table I. It will be noted that one of the isolates of *Chaetomium globosum* taken for this study is the fungus employed by the Australian mycologists as a test organism for the evaluation of war service materials. Two other isolates for *C. globosum* and of *C. cochliodes* were secured from the Panama Canal area.

During the course of this investigation three new species of *Chaetomium* were used in the experimental work; their descriptions are given at this time accompanied with illustrations.

Type specimens have been deposited at the Farlow Herbarium, Cambridge, Massachusetts, subcultures have been deposited at the New York Botanical Garden, Bronx Park, New York, as well as in the Mycological Herbarium of the U. S. Department of Agriculture located at the Plant Industry Station, Beltsville, Maryland.

Chaetomium dolichotrichum Ames, sp. nov. (FIG. 5: 8–10)

Perithecio nigro, parvo, globoso vel ovato-globoso 80 × 85 (50–90 × 52–95), cum substrato laxius connato. Pilis lateralibus haud numerosis, laevibus, flexuosis. Pilis terminalibus dimorphicis, quorum majoribus in capitulo denso aggregatis, dichotome ramosis, ramis late patentibus, sub angulo acuto divergentibus, basi nigris ca. 6.5 μ crassis, in apicem gracilem terminantibus; minoribus terminalibus, paucioribus, gracilibus, nigris, apicem sporiferum longius excendentibus, interdum ramosis, ca. 2–2.5 μ diametro.

Type locality, Cades Cove, the Great Smoky Mts., Tenn.

Chaetomium microcephalum Ames, sp. nov. (FIG. 6: 4–7)

Perithecio albido vel griseo, alto, gracili 250 × 120 μ (200–400 × 80–140) cum substrato laxius connato. Sporis exudatis ad apicem perithecii capitulatim congregatis. Pilis lateralibus numerosis, apice collapsibilibus, manifeste septatis. Pilis terminalibus crassioribus simplicibus vel ramosis, septatis. Pilis ramosis basi latis 7.5–8.5 μ subinde in apicem gracilem acutatis, undulatis spiralibusve, circumvolutionibus 2–4. Sporis maturis pallidis, brunneo-olivaceis, ovalibus, utrinque apiculatis vel uno apice rotundatis.

Type locality: Cades Cove, The Great Smoky Mts., Tenn.

Chaetomium pachypodioides Ames, sp. nov. (FIG. 7: 1–3)

Perithecio nigro, magno, alto, elongato, basi saepissime crassiore, ad apicem angustato 350 × 150 μ (250–475 × 120–200) in subiculo insidenti e rhizoideis atre brunneo-olivaceis vel nigris efformato, apicibus sporiferis interdum breviter cirrhosis. Pilis lateralibus sat numerosis, acanthoideis, acuminatis,

septatis. Pilis terminalibus apicem sporiferum valde excedentibus, numerosis, acuminatis, undulatis spiralibusve, septatis, minute granulosis, basi ca. 6 μ crassis, in apicem ecòloratum terminatis. Ascosporis maturis pallidis brunneo-olivaceis, formam *Citri Lemoni* mentientibus, utrinque apiculatis.

Type locality, Cades Cove, The Great Smoky Mts., Tenn.

EXPERIMENTAL RESULTS

Comparisons of the influence on breaking strength of these sixteen species of *Chaetomium* as grown on the media described is summarized in table II.

TABLE II

EFFECT OF DIFFERENT SPECIES OF CHAETOMIUM, GROWN ON FOUR NITROGEN SOURCES, ON THE BREAKING STRENGTH OF 8-OUNCE COTTON DUCK, AFTER 7 DAYS' INCUBATION

Species	Isolate number	Residual breaking strength as per cent of the original				Physiological groups
		$NaNO_3$	NH_4NO_3	$(NH_4)_2SO_4$	$NH_4H_2PO_4$	
C. globosum	1042.4	7.6	13.9	21.2	24.1	I
C. globosum	1042.5	9.1	11.4	20 2	28.8	I
C. globosum	1042.6	18.6	11.6	23.3	27.4	I
C. globosum	1042.7	18.6	19.1	20.0	25.2	I
C. caprinum	1043.0	10.8	10.1	15.8	33.6	I
C. cancroideum	1044.4	25.2	10.6	26.0	21.4	II
C. dolichotrichum	1044.7	37.0	19.6	20.9	20.0	III
C. funicolum	1043.1	49.7	21.9	20.9	18.0	III
C. funicolum	1043.2	48.2	15.3	19.9	13.6	III
C. elatum	1043.4	45.0	28.6	28.5	32.9	III
C. elatum	1043.5	47.9	22.6	19.6	34.5	III
C. contortum	1044.9	34.8	25.2	28.7	27.5	III
C. bostrychodes	1045.1	22.9	20.2	23.9	23.9	IV
C. cochliodes	1043.6	44.3	51.3	54.7	55.0	IV
C. cochliodes	1043.7	54.9	43.4	48.0	61.9	IV
C. murorum	1044.8	43.7	45.2	46.7	48.9	IV
C. ochraceum	1044.5	44.4	54.1	54.4	55.6	IV
C. aterrimum	1043.8	50.9	45.9	44.5	45.3	IV
C. aureum	1043.9	50.5	45.5	60.6	62.1	IV
C. pachypodioides	1044.3	74.9	70.3	38.4	33.1	V
C. convolutum	1044.0	89.6	87.9	89.9	82.7	VI
C. microcephalum	1045.0	91.3	54.0	100.0	100.0	VII
pH of original autoclaved medium:		7.1	6.6	5.8	5.5	
pH of medium at harvest		6.7–8.4	5.8–6.6	4.6–5.8	4.3–5.5	

The results presented in table II show that the *Chaetomium* species vary in their ability to decompose cellulose and in their reaction to different nitrogen sources. It is observed that there is variation between several isolates of some species; further

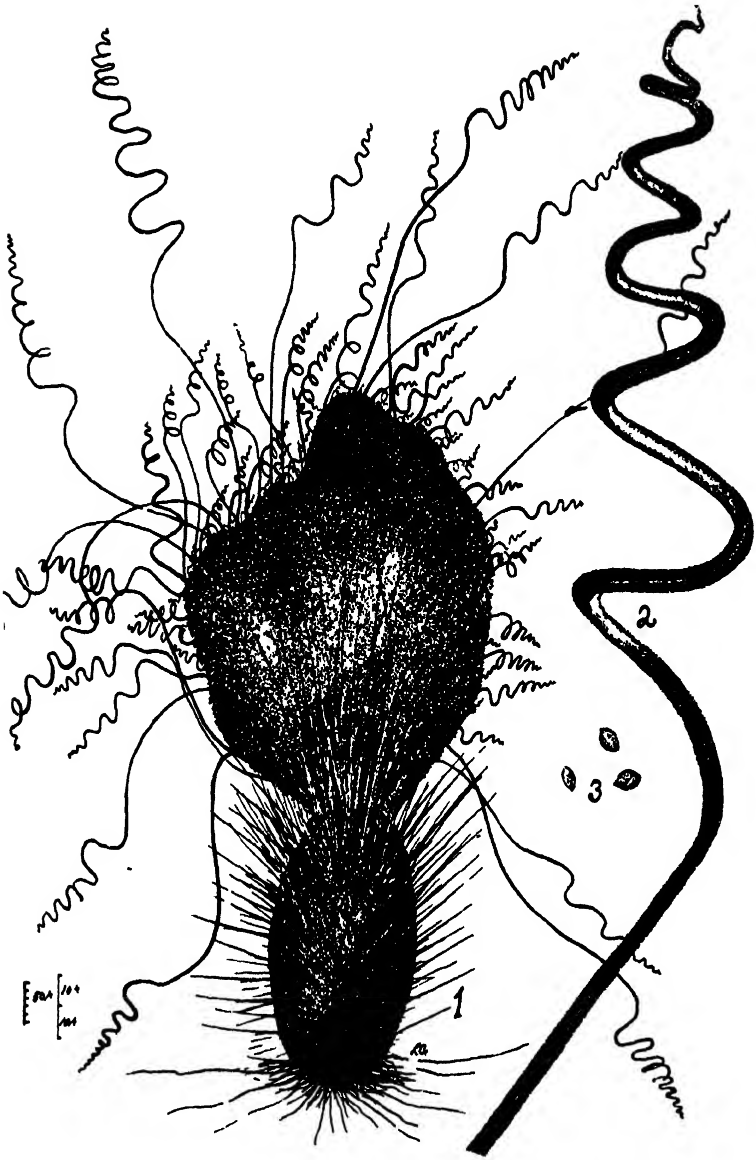

FIG. 4. *Chaetomium convolutum* Chivers; 1, mature perithecium, 2, terminal hair; 3, mature ascospores.

studies of such variation may be of interest. On the basis of results obtained an arbitrary classification into physiological groups has been made for convenience of discussion. Information on the following groups is based upon the conditions of our tests, *i.e.*, using 4 nitrogen sources and an incubation period of 7 days.

Group I includes *C. globosum* and *C. caprinum* which are very active cellulose decomposers that produce slightly greater losses in breaking strength on a nitrogen source, $NaNO_3$, that ranges on the alkaline side of neutrality following the utilization of the NO_3 radical by the fungus.

Group II is represented by *C. cancroideum*, morphologically similar to *C. funicolum*, which is an active cellulose decomposer that seems to be most active on a neutral to slightly acid medium, NH_4NO_3.

Group III contains *C. dolichotrichum*, *C. funicolum*, *C. elatum*, and *C. contortum* which are active cellulose destroyers that thrive especially well on the more acid nitrogen sources, NH_4NO_3, $(NH_4)_2SO_4$, and $NH_4H_2PO_4$.

Group IV is characterized by species that are active to moderately active in destroying cellulose and that have no marked preference for nitrogen sources.

Group V is restricted in its preference of nitrogen source to $(NH_4)_2SO_4$ and $NH_4H_2PO_4$ on which it produces moderate losses in breaking strength of the cotton fabric.

Group VI represented by *C. convolutum* is a relatively inactive cellulose decomposer.

Group VII is represented by *C. microcephalum*. It seems to be restricted in its ability to decompose cellulose under these experimental conditions to a very narrow limit, *i.e.* NH_4NO_3 medium.

Several other isolates of *Chaetomium* were studied and found to be inactive as cellulose decomposers. Among these were two species received under the name *C. trigonosporum* and *C. caninum* received from J. D. Machacek, Dominion Laboratory of Plant Pathology, Winnipeg, Man. These species failed to grow on any mineral salts-cellulose media tested. Slight differences in the

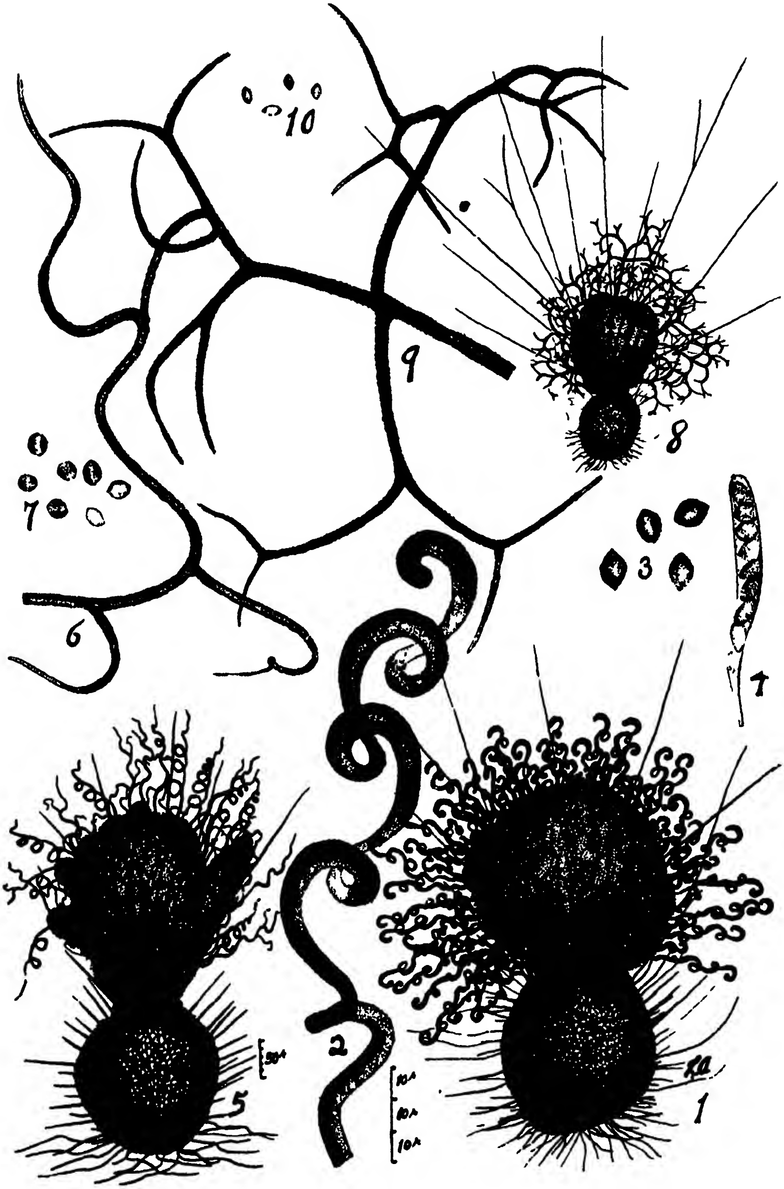

FIG. 5. 1–4, *Chaetomium contortum* Peck; 1, mature perithecium; 2, terminal hair; 3, mature ascospores; 4, ascus containing immature ascospores; 5–7, *Chaetomium bostrychodes* Zopf; 5, mature perithecium; 6, terminal hair; 7, mature ascospores; 8–10, *Chaetomium dolichotrichum* Ames; 8, mature perithecium; 9, terminal hair; 10, mature ascospores.

ability of different isolates of the same species of *Chaetomium* to deteriorate cellulose may be observed from data presented in table II.

DISCUSSION

The impact of war has brought to a focus the necessity of learning the characteristics of the causal agents in the decomposition of cotton fabrics and necessitates the determination of means of preventing fabric destruction. The study here presented is a beginning in this direction and is chiefly concerned with the study of the ability of various species of *Chaetomium* in decomposing cotton duck within a specified period of time.

Thom et al. (**28**) secured quantitative data that represent the ability of several *Chaetomium* species to destroy cellulose. In addition to *C. globosum* they tested *C. cochliodes*, *C. funicolum*, and *C. aureum* on one nutrient medium which is similar to the one used in this investigation when $NaNO_3$ is used as the nitrogen source. They found that *C. globosum*, *C. cochliodes*, *C. funicolum*, and *C. aureum* produced 94.5, 91.6, 89.7, and 88.0 per cent loss in breaking strength of 8-ounce cotton duck after 14 days incubation, respectively. In the present investigation, the same species of *Chaetomium* when grown on the $NaNO_3$ medium, Table II, produced 92.4, 50.4, 49.1, and 49.5 per cent less in breaking strength after 7 days incubation period. Culture transfers from the same *C. globosum* isolate used by Thom et al were used in this study and thus may account for the close similarity in results for this species. The cause of the differences obtained between the two investigations with the other three species is not known. It may be due to intra specific variations.

The loss in breaking strength of cotton duck resulting from the growth of *C. globosum* and *C. elatum* on $NaNO_3$, NH_4NO_3 and $NH_4H_2PO_4$ as the nitrogen source media was reported by Greathouse et al (**15**). These investigators found that *C. globosum* gave a loss in fabric breaking strength of 118 pounds with $NaNO_3$, 108 pounds with NH_4NO_3 and 96 pounds with $NH_4H_2PO_4$ as nitrogen sources. On the other hand, the growth of *C. elatum* under similar conditions resulted in losses of 67, 89, and 88 pounds, respectively. The results with these two species show that the nitrogen source is an important factor in determining

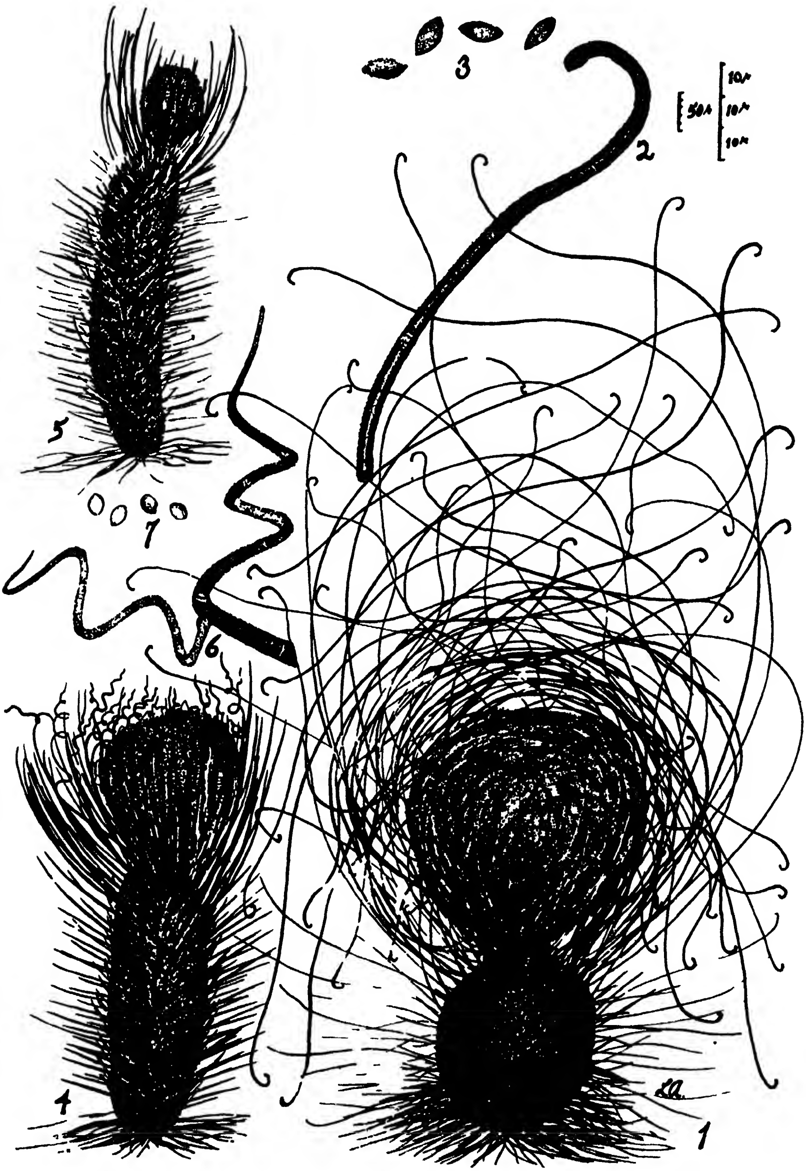

FIG. 6. 1–3, *Chaetomium murorum* Corda; 1, mature perithecium; 2, terminal hair; 3, mature ascospores; 4–7, *Chaetomium microcephalum* Ames; 4–5, mature perithecia; 6, terminal hair; 7, mature ascospores.

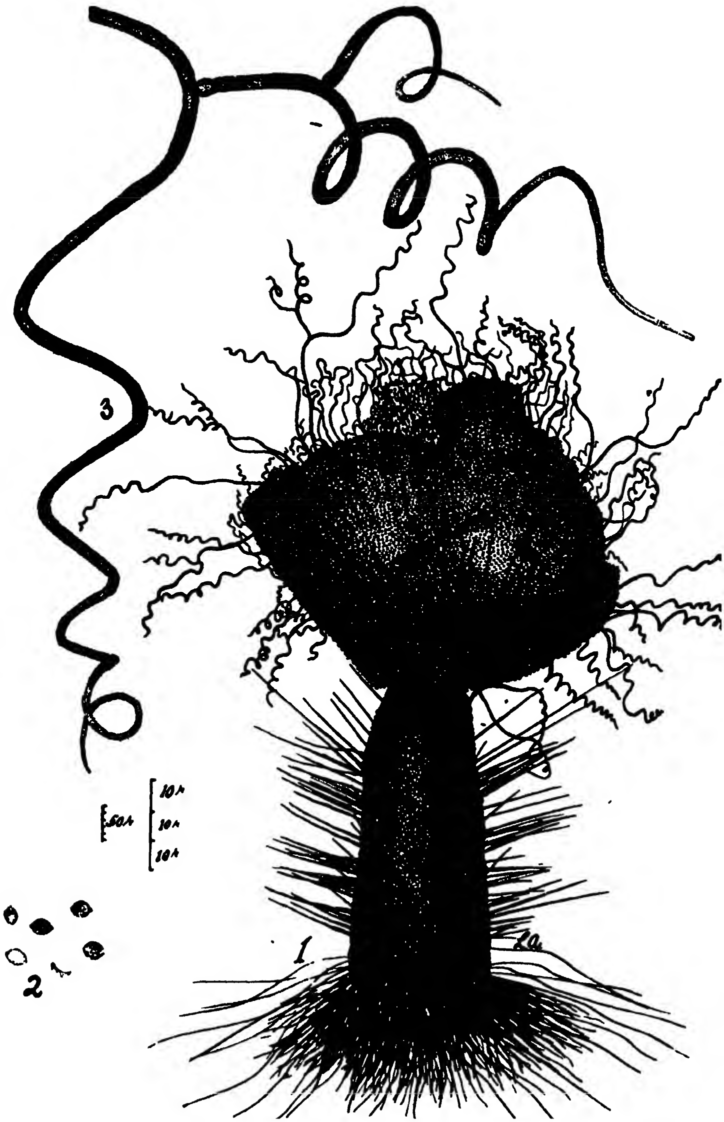

FIG. 7. *Chaetomium pachypodioides* Ames; 1, mature perithecium; 2. mature ascospores; 3. terminal hair.

the response of cellulose-decomposing fungi. This phenomenon is even more strikingly demonstrated from the data presented in table II where a comparison of sixteen different *Chaetomium* species was made. Most *Chaetomium* species, like fungi in general, grow best on media neutral or slightly acid in reaction.

C. globosum, the fungus chosen as the test organism by Thom et al (**28**), is characteristic of the genus *Chaetomium* in decomposing cellulose, with the possible exception that it thrives best in a slightly alkaline medium, which is the exception rather than the general rule among *Chaetomium* species as well as fungi in general. The organism to be used in testing fabrics for mildew resistance should be capable of rapid destruction; it should be stable in its cultural and cellulose destroying characteristics; its response to specific factors, *i.e.* pH, temperature, fabric preservative, etc., should have been established; and its distribution and occurrence in nature should be known. *C. globosum*, as well as several of the other *Chaetomium* species, meet the majority of these requirements.

SUMMARY

1. Sixteen species of *Chaetomium* have been tested to determine their ability to decompose cotton fabric. Enumerated in a descending order according to their deteriorating ability they are: *C. globosum*, *C. caprinum*, *C. cancroideum*, *C. dolichotrichum*, *C. funicolum*, *C. elatum*, *C. contortum*, *C. bostrychodes*, *C. cochliodes*, *C. murorum*, *C. ochraceum*, *C. aterrimum*, *C. aureum*, *C. pachypodioides*, *C. convolutum*, *C. microcephalum*.

2. Three new species of *Chaetomium* have been described, *C. dolichotrichum* Ames, *C. pachypodioides* Ames, and *C. microcephalum* Ames.

3. The ability of the sixteen species of *Chaetomium* to decompose cellulose fabric in the presence of a standard nutrient salt medium in which the source of nitrogen was obtained from four different sources ($NaNO_3$, NH_4NO_3, $(NH_4)_2SO_4$, and $NH_4H_2PO_4$) were studied. It was found that the sixteen species studied fall into seven groups based upon their ability to utilize the cotton fabric in the presence of different nitrogen sources. The percentage of loss in breaking strength of the fabric following a

seven day incubation of each isolate was the criteria used for physiological differentiation between species.

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EXPLANATION OF FIGURES

All figures have been outlined by the aid of a camera lucida. The perithecia are all drawn to the same scale under low power, a scale being included on each plate. The detailed drawings of terminal hairs and spores were drawn under the high power objective and a scale in microns is included on each plate so that direct measurements can be made.

NOTES AND BRIEF ARTICLES

HYDNUM FLORIFORME IN FLORIDA

This beautiful species was collected by the author under laurel oaks in Gainesville during the summer of 1944. Originally described from Bavaria by Schaeffer, it had been found in dry woods from New England southward to Alabama. *H. aurantiacum* Alb. & Schw. is not distinct. Although assigned to both *Hydnellum* and *Calodon*, it properly belongs in the latter. Miller says the two genera are not sufficiently distinct anyway. I sent a specimen to Dr. Coker, who kindly verified my determination.—W. A. MURRILL.

GIANT PUFFBALL IN MAINE

Worthy of note are the following data on a specimen of Giant Puffball (*Calvatia gigantea* Batsch.) collected in Brewer, Maine, on August 27, 1943, by Mr. A. L. Hodgkins. The specimen had a girth of 46 inches, diameter of approximately 14.5 inches, height of 9 inches, and weight of 7.5 pounds at the time of collection. After air-drying in a warm room for nearly a year the weight dropped to .5 pound. Although much larger puffballs have been recorded,[1] those of the size noted above are certainly rarely met with in this vicinity.—F. HYLAND.

Announcement is made of the publication of a lithoprint edition of the classical Sylloge Fungorum of Saccardo, under license from the alien property custodian. The work is issued in twenty-five (25) volumes bound in twenty-seven as originally published. In the interests of economy both from the standpoint of paper and printing costs the printing surface of the volumes has been reduced seven per cent. This, however, does not appreciably affect the readability of the text. The paper used was especially selected for the purpose and was tested by the United States

[1] The weight of the Ottawa specimen is recorded as 18.75 pounds. (See Mushrooms and Toadstools by H. T. Güssow and W. S. Odell. Ottawa, 1927.)

National Bureau of Standards. The volumes are bound in library buckram.

Further information may be secured from the firm of Edwards Bros., Inc., Ann Arbor, Michigan.

A NEW POLYPORE FROM UTAH

The species described below was sent to me by Dr. Rhoads. It is tomentose like *P. maculosus* Murr. but resembles *P. elegans* Fries in spore characters.

Polyporus submaculosus sp. nov.

Pileo 3 cm. lato, tomentoso, fumoso, badio-maculato; tubulis 1 mm. longis, poris 4 per mm., angulatis, albis, demum isabellinis; sporis oblongis, 10 × 3 μ; stipite excentrico, nigro, 1 × 0.5 cm.

Pileus subcircular, slightly depressed, solitary, 3 × 3 × 0.5 cm.; surface covered with thin fumose tomentum except near the undulate entire margin, where there are small glabrous bay spots; context tough to corky, white, homogeneous, 4 mm. thick; tubes decurrent, 1 mm. long, mouths 4 per mm., thin-walled, angular, white to pale-isabelline; spores oblong, smooth, hyaline, about 10 × 3 μ; stipe eccentric, solid, woody, equal, minutely velvety, chestnut-black, about 1 × 0.5 cm.

Type collected by A. S. Rhoads on a dead fallen stem of trembling aspen above Ogden Dam, Weber Co., Utah, Sep. 3, 1944 (*F 19210*).—W. A. MURRILL.

WILLIAM TITUS HORNE

William Titus Horne, Professor of Plant Pathology in the University of California, died on April 12, 1944 in his sixty-seventh year. He was a graduate of the University of Nebraska with a Bachelor of Science degree in 1898. He served as instructor in the Nebraska Wesleyan University and University of Nebraska Farm School. He took graduate study at Columbia University and then served at the Cuban Agricultural Experiment Station as assistant and then chief of the Department of Plant Pathology from 1904 to 1909 where he married Mary Tracy Earle, sister of the late Professor F. S. Earle. He came to the University of California at Berkeley as Assistant Professor of Plant Pathology

in 1909 and was acting Head of the Division of Plant Pathology in 1919–20. He transferred his activities to the Citrus Experiment Station in 1928, where he became Associate Professor and then Professor of Plant Pathology. Here he had a long and useful service especially in the field of avocado and subtropical diseases.

In 1938 he was elected President of the Pacific Division of the American Pathological Society. He was a member of the American Association for Advancement of Science, American Phytopathological Society, California Botanical Society, Torrey Botanical Club, Mycological Society of America, Sigma Xi and Alpha Zeta.

One of his most important publications since coming to Riverside was his 1934 Bulletin on Avocado Diseases. He had ready at his death a completed manuscript on the Diseases of the Guava, which is being edited for publication by the University of California.—H. S. FAWCETT.

David Gruby and the Centenary of Medical Mycology, 1841–1941. Six papers published during the years 1841–1844 constitute the contribution of David Gruby to Medical Mycology. They also form, according to our authors,[1] the very foundation stones of that science. In the first of these papers was described the causative fungus of favus. Later papers announced the discovery of the cause of ringworm of the scalp, ringworm of the beard and thrush. In appropriate recognition of the centenary of their original publication these papers are published for the first time in English translation. The translation and explanatory notes are the work of Dr. Benedek.

On reading these papers, one is impressed by the fact that the author was not only a careful observer but an enthusiastic experimenter. One paragraph from the second paper on favus may be quoted in this connection.

"I carried out," he says, "inoculation on thirty phanerogamic plants; I succeeded only once. On 24 silkworms, I did not obtain any results. On six reptiles, I likewise failed. On four birds and

[1] Zakon, S. J. and T. Benedek. Bulletin of the History of Medicine 16: 155–168. 1944.

on eight mammals, no results. In my first experiment on humans I inoculated Prof. Rinneker, of Wurzburg, on the arm; this inoculation produced a slow inflammation and a slight suppuration. I inoculated myself four times with the same results. In total, in 77 inoculations I obtained a result on one plant only, this unique fact, however, seems to me interesting in giving an example of a human disease communicable to a vegetable."

Introductory to the papers there is a brief sketch of the life of Dr. Gruby (1810–1898), with citations of longer biographies and a portrait. The authors of this article and the editors of the Bulletin of the History of Medicine have done a distinct service in calling attention to this pioneer and in making his contributions readily available in English.—NEIL E. STEVENS.

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CYLINDRIC SPORES IN AMANITA

Species of *Amanita* abound in northern temperate regions but all of them have globose, ovoid or ellipsoid spores. In publishing *A. roanokensis* Coker first brought to the attention of mycologists a species with cylindric spores. The second species of this group was described by Beardslee as *A. cylindrispora*. Since then the author has added eight others to the list, all from Florida.

Since the geological history of Florida is recent and there is no indication of the introduction of cylindrosporous forms from tropical America, it is safe to assume that these forms are endemic to Florida and the extension of the coastal plain northward to North Carolina. What appeals to me as of special interest is the fact that this group, obviously of recent origin, has followed the lines of development already so well known in the older species.

In a brief article like this I can only touch upon some of the main points. Take the Verna Group, for example. Here we have the old and widely distributed species, *A. verna*, with globose spores, to which I have added *A. vernella* and *A. suballiacea*. Ellipsoid spores in this group are found in *A. pseudoverna* and *A. verniformis;* while cylindric spores occur in *A. margarita* and *A. tenuifolia*. At first sight, some of these would be referred to *A. verna* without question, but the microscope at once reveals differences.

Several other groups show similar parallels. *A. cylindrispora* has cylindric spores while those of *A. cylindrisporiformis* are ellipsoid. For *A. parva* the counterpart is *A. parviformis;* for *A. praelongispora*, *A. virosa* and *A. virosiformis*, both with ellipsoid spores.

In the large Solitaria Group, so well represented in Florida, the parallel is fully as striking. *A. solitaria*, *A. strobiliformis*, etc. with ellipsoid spores have their perfect counterparts macroscopically in *A. solitariiformis*, *A. Rhoadsii*, etc. with cylindric spores. This is a rich field for observation because biologic groups of recent origin tend to exhibit rapid development and wide variation.

This variation is well illustrated in the odors met with in several Florida species of this genus. Some of them are decidedly strong and persist in the herbarium for years. Others are so unique that it is impossible to describe them. The chemistry of the Florida amanitás must be left to someone with good equipment and plenty of time. I have no doubt that work in this field would prove very absorbing and yield important results.—W. A. MURRILL.

TWO ORTHOGRAPHIC ERRORS IN FUNGOUS NAMES

ALLOMYCES ARBUSCULA Butler.

In a footnote on p. 78 of his monograph of *Allomyces*,[1] Emerson alters the specific epithet of *A. arbuscula* Butler to *arbusculus*, "to agree in gender with the generic name," citing Article 72(2) of the International Rules of Botanical Nomenclature, in which compounds of *-myces* are said to be masculine. *Arbuscula*, however, is not an adjective, but a noun in apposition, meaning "a small tree or shrub," and Butler's binomial was consequently correct. Emerson's variety *arbusculus* (l.c., p. 132) must be written var. *arbuscula*, since it is "a clearly unintentional orthographic error" in the sense of Article 70 of the Rules. Unfortunately the proposed alteration in the specific epithet has been taken up by Sparrow in his Aquatic Phycomycetes, and by others in recent papers, e.g., McCranie (Mycologia **34**: 212. 1942),

[1] Emerson, Ralph. An experimental study of the life cycles and taxonomy of *Allomyces*. Lloydia **4**: 77–144. 1941.

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OBSERVATIONS ON THE GENUS CATENARIA [1]

JOHN N. COUCH

(WITH 78 FIGURES)

INTRODUCTION

In soil from the Gulf States collected in January 1942, a fungus was found growing within the threads of *Allomyces anomalus* unlike any parasite previously seen. Many of the threads of *Allomyces* were filled from base to tip with ovoid or spherical, colorless or pale brown *Olpidium*-like bodies (FIG. 2). Subcultures of the infected *Allomyces* were made, but before observations were carried out, the cultures had dried. Upon the addition of water, the pale brown bodies of the parasite germinated, much as in *Blastocladiella cystogena*. Observation showed that the resting sporangia, as well as the zoosporangia, were not formed singly as in *Olpidium*, but were connected one to another by narrow isthmuses exactly as in *Catenaria Anguillulae*. Here apparently was a fungus connecting the *Blastocladiales* with *Catenaria* which might throw some light on that still inadequately known genus. It is the purpose of this paper to describe the new parasite on *Allomyces* and to report some heretofore unknown facts in the life history of *Catenaria Anguillulae* which will help to clear up the confusion about that genus.

[1] Address of the President, 1943, Mycological Society of America, Cleveland, Ohio, September 14, 1944.

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OBSERVATIONS ON CATENARIA ALLOMYCIS

The new fungus, which I will call *Catenaria Allomycis,* was purified by adding the zoospores of the parasite sucked up in a capillary pipet to water cultures of the *Allomyces* growing on hemp seed. The water cultures of the host were descended from a pure culture on agar F_{13}. All attempts to culture the parasite with or without its host on agar have resulted in failure. Some of the agars tried were 0.5 per cent plain agar, 1 per cent agar plus a trace of peptone, F_{13} agar (first used by Foust for the successful growth of *Allomyces* and its parasite *Rozella Allomycis*) and various strengths of liver agar with and without various sugars (for formulas see below under *C. Anguillulae*). For a fungal parasite to be transmitted through its host on solid media it must be capable of producing schizonts which spread through the host. *R. Allomycis* does this, while *C. Allomycis* does not. All attempts to culture *C. Allomycis* on cooked plant material, as several kinds of grass leaves, onion leaves and roots, and cooked animals as nematodes and fluke eggs failed.

The parasite first found on *Allomyces anomalus* has been transferred to all other species of *Allomyces.* It grows well on both the gametophytic and sporophytic generations of *A. arbusculus* and *A. javanicus,* having the same appearance as on the original host. However, it attacks *A. javanicus* so greedily that by the second generation, the host is destroyed before it can form resting bodies. It is doubtful if the parasite could survive in nature on this plant. On *A. moniliformis* it is a less vigorous parasite than on *A. anomalus,* and produces many resting bodies singly in the zoosporangia of the host (FIG. 12). The parasite grows well on *Blastocladiella simplex* Matthews, but not at all on *B. cystogena, B. laevisperma,* or *B. asperosperma.* It failed to grow on *Blastocladia parva, Catenaria Anguillulae, Achlya caroliniana,* and *Saprolegnia parasitica.*

Resting bodies of the parasite retain their vitality dried for a year and perhaps much longer. Stock material for study and experimental purposes is prepared simply by allowing infected cultures of *Allomyces* to dry up in a Petri dish. If charcoal water is added, the resting sporangia of both host and parasite begin to germinate in a few hours (10–24) and new cultures are made by adding

pieces of boiled hemp seed. A simple procedure has been to add water and hemp seed to dried cultures late in the afternoon and by the following morning the resting bodies would show all stages of germination.

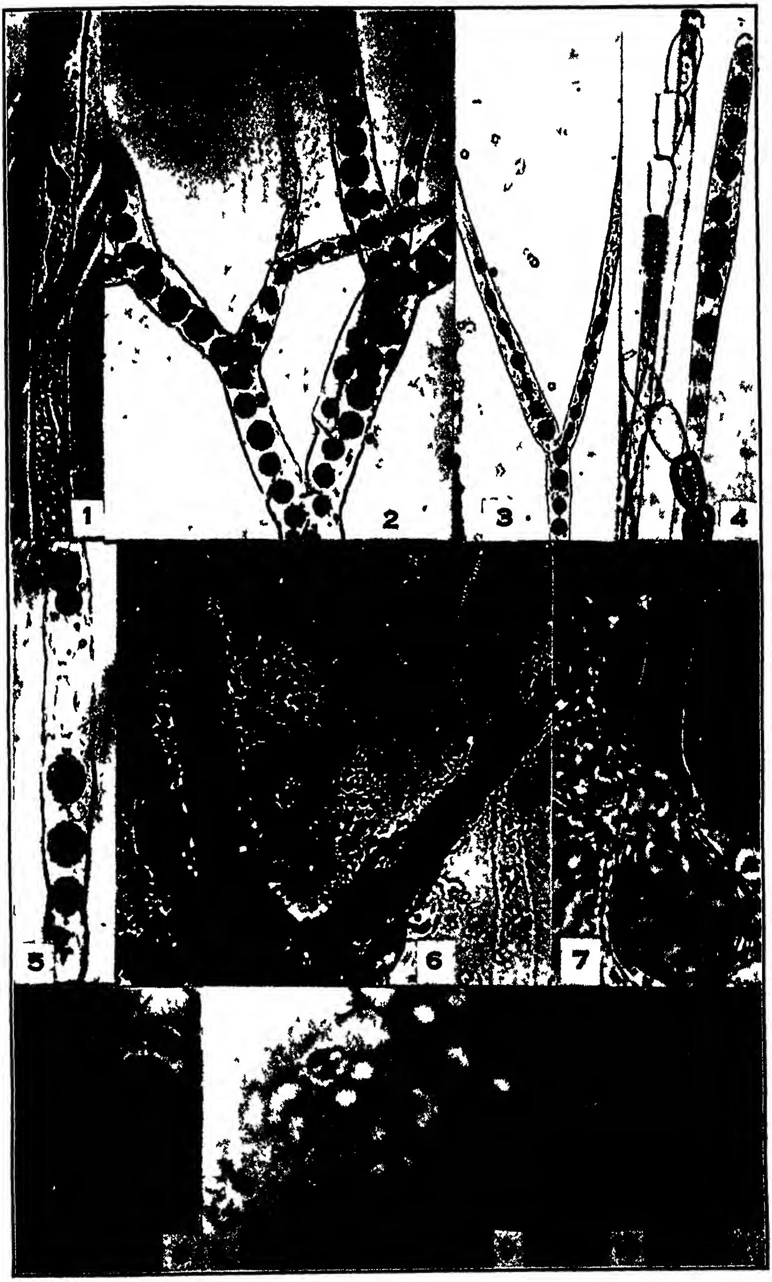
Experiments have shown that the resting bodies in any given culture are not ready for germination all at the same time. Six cultures dried for 22 days showed 5–10 per cent germination of the resting bodies when water was added. These six were dried again, and after two months showed a total resting body germination of 15–20 per cent. Immediately after the observations were made the six cultures were dried again, this time for five months. Upon the addition of water and after a lapse of 36 hours, all six contained vast numbers of germinating resting bodies.

In germinating, the resting body absorbs water, the fat bodies become more or less uniform in size and are more evenly distributed in the cytoplasm. The swelling of the contents causes the outer wall of the resting body to crack on one side into several irregular lobes and through this opening a broad tube pushes (FIG. 35). This penetrates the host wall through a large opening and may extend out to a length of 50–several hundred microns (FIGS. 6, 7, 37–40). The development of the resting body zoospores is similar to that of the regular zoospores, except that here the fat bodies are more abundant and are collected in a sphere some time before the spores emerge (FIGS. 36–40). A similar condition has been shown in *Blastocladiella simplex* for the zoospores by Matthews (1937) and in *Allomyces arbusculus* for the gametes by Hatch (1935). When mature, the tip of the tube gelatinizes and the resting body zoospores emerge, the first ones usually collecting in a ball. As in *Blastocladiella cystogena,* the resting body zoospores are furnished with cilia, one to each spore, and are capable of a little sluggish swimming, but never progress far from the tip before encysting (FIG. 37). As a rule, the resting body zoospores encyst at the tip in an irregular compact mass (FIGS. 38–40). Each spore contains a nucleus, nuclear cap and many fat bodies (FIG. 37).

After about two hours, the contents of the cysts divide into four gametes, which emerge through a short papilla (FIGS. 6, 8, 9, 38–41). They usually remain for several minutes at the tip of the papilla, their cilia projecting straight out and occasionally lashing

in a futile fashion (FIG. 41). Sometimes one may break from the cluster and swim or crawl away, or rarely the entire cluster of four may swim awkwardly away like a colony of *Pascheriella.* Usually some of the gametes remain stationary at the exit pore while others creep about over the entire mass. When two compatible gametes come together side by side with their cilia pointed in the same direction, they fuse so rapidly that the actual process is easily overlooked. The two membranes become one, the nuclear caps fuse and then the nuclei unite. The shiny globules do not unite but all collect on one side of the zygote and toward the posterior end. The two cilia do not unite but, as in *Blastocladiella cystogena,* become so closely appressed one to another as to appear as one and act as one in swimming (FIGS. 10, 11, 41, 42). At times when the zygote pauses for a moment, the two cilia can be seen under the dark field to separate for a moment and lash independently. Stained preparations also show two distinct cilia (FIGS. 10, 42).

There is much variation in the behavior of the gametes. A few special cases will be described. Three quiet gametes were selected for observation. Two or three minutes later one became active and began crawling about over the other two, and then suddenly broke loose and swam away. The other two remained in contact with very gentle ciliary motion for about five minutes, and then began fusing. As this progressed, the immature zygote became active and swam away before fusion was entirely complete. This observation is of interest because it shows that two compatible gametes may lie in contact some time before fusing. Other observations indicated that sometimes gametes may behave as males and females. This was the case with a gamete found sitting on a cyst. It was inactive except for an occasional lash of its flagellum. Soon another gamete, a male (?) swam up, and began creeping over the surface of the female. About two minutes later a second male came on the scene and immediately both began fusing with the female. However, the first gamete to arrive had the better start and as the zygote took form, it succeeded in jerking loose from the second male. The above description of gamete formation and fusion is strikingly similar to the behavior in *Blastocladiella cystogena* (Couch & Whiffen, 1942).



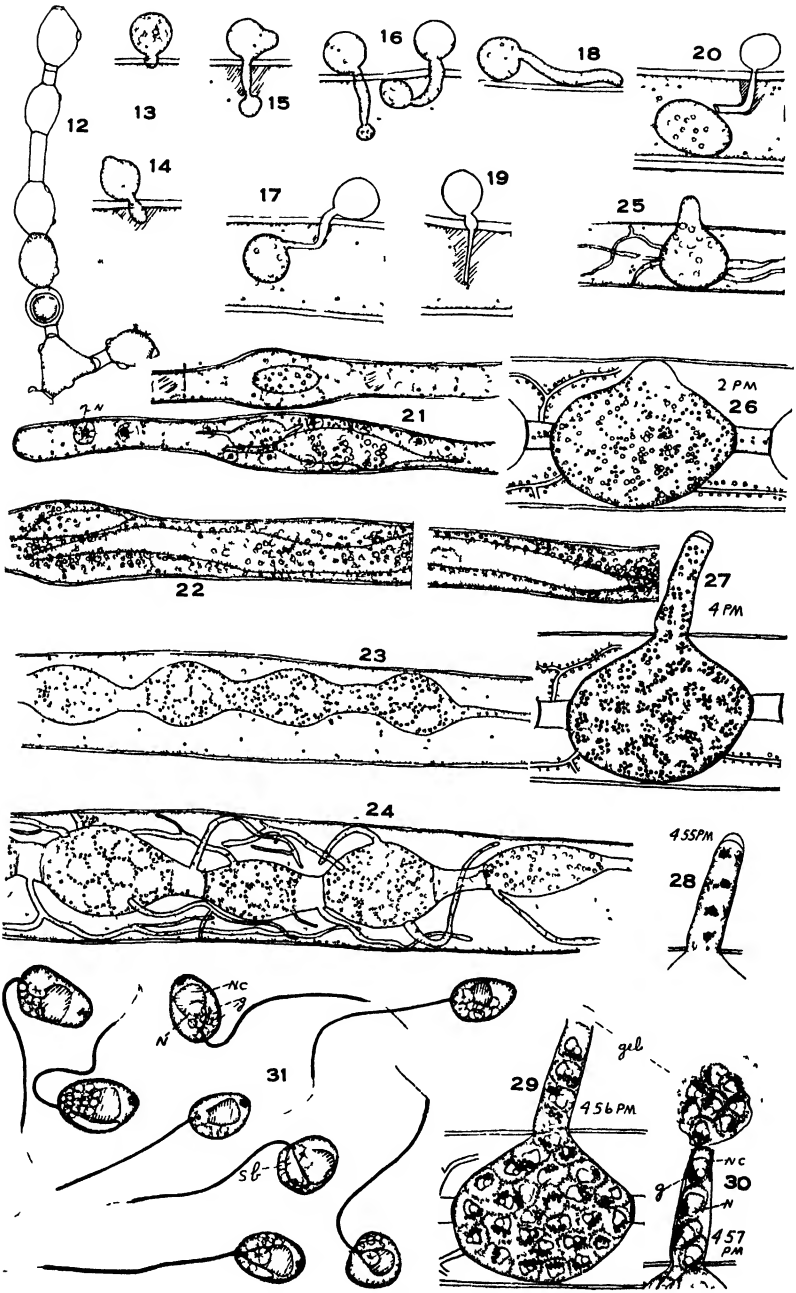
FIGS. 1–11. *Catenaria Allomycis.*

The zygote is a vigorous swimmer. Eventually it comes to rest on the surface of the host, loses its cilia, rounds up, encysts, and sends a fine penetration tube into the host thread (FIGS. 13, 44). As the tube grows, the host deposits considerable callus material around the tube but only seldom is its growth checked (FIGS. 17, 19, 20). If no host is present, the zygote may form a germ tube in water, exactly like the one that penetrates the host. This tube grows to a maximum length equal to about twice the diameter of the zygote, and then changes to a zoosporangium to form two zoospores.

The infecting body is round at first but soon elongates (FIG. 20), becoming somewhat spindle-shaped (FIG. 21). The ends continue to grow, extending lengthwise in the host thread until a long, irregular, tubular structure, usually unbranched, is formed (FIG. 22). It is very difficult to make out the limits of the parasitic thallus at this stage, for it is surrounded by the fat bodies and protoplasm of the host. It appears that the immature thallus is devoid of rhizoids. When it has attained mature length, swellings begin to form at more or less regular intervals (FIG. 23). When these are about mature in size, septa are laid down separating the swellings from one another. At first only one septum is laid down between two swellings, and this is always at the end of the isthmus and never in the middle (FIG. 24). A few minutes later, after most of the protoplasm has moved from the isthmus into the swollen part, another septum is formed separating the isthmus from the swelling. The enlarged parts become the zoosporangia or resting sporangia and the narrow parts the isthmuses (FIGS. 24, 26).

The rhizoids are thick, stubby structures, and apparently are not developed until after the thallus becomes septate. They are usually surrounded by the granular or fatty material of the host (FIGS. 26, 27). In figure 24 the rhizoids are exceptionally well developed. On the thalli shown in figures 21–23 no rhizoids could be detected. The young thallus apparently absorbs its food over its entire surface. The rhizoids in this species are perhaps vestigial structures.

The mature thallus of the parasite typically consists of a single, usually unbranched catenulate hypha within the host. However, a single host hypha may contain two or even several moniliform



FIGS. 12–31. *Catenaria Allomycis.*

parasite thalli (FIG. 32) or the thalli may be clustered in a swollen portion of the host thread (FIG. 33).

The first infections of a young culture by the zygotes of *Catenaria Allomycis* produce parasitic thalli consisting entirely of zoosporangia. The zoospores formed in these sporangia give rise to thalli that may be part zoosporangia and part resting bodies and the later formed zoospores give rise to thalli consisting entirely of resting bodies. It seems that resting body formation is brought on by the exhaustion of the host thallus and a reduction of the food, as Barrett (1912) suggested in *Olpidiopsis*. Evidence for this conclusion is that it is possible to keep zoosporangial thalli going constantly by adding fresh hemp seed daily so that new young *Allomyces* will always be present.

Just before sporangial formation, the protoplasm moves from the isthmuses into the swellings and these become separated from the isthmuses by cross walls (FIG. 24). The swollen parts become the zoosporangia or resting sporangia. The protoplasm at this stage contains numerous vacuoles and fat bodies of variable size. A sporangium mature in size had the appearance shown in figure 26. The emergence tube had just begun to grow out. Two hours later (FIG. 27), the tube was formed and the fat bodies, now all of about the same size, were arranged in clusters of about eight. Each cluster of fat bodies indicated the center of a spore origin. Vacuoles at this stage were doubtless present, but very indistinct. About an hour later (FIG. 28), the protoplasm showed a very homogeneous condition, except for the fat bodies. During this phase, a new moon-shaped body appeared in the cytoplasm. This quickly enlarged and formed the nuclear cap, surrounding half of the nucleus which meanwhile had become distinct. As the nuclear caps formed, the spores became very distinct and were polygonal from pressure (FIG. 29). While this was happening (and taking only a few seconds), the tip gelatinized and suddenly the end spore followed by others pushed out into a spherical gelatinous envelope formed from the gelatinizing tip (FIGS. 29, 30). For a few seconds the spores in the sphere remained quiet, but soon became active, broke through the surrounding gelatine, and swam away with a single posterior cilium. The remaining spores with the pressure now released became very active, swimming about in the sporangium and push-

ing up into and through the tube to the outside, to swim away immediately.

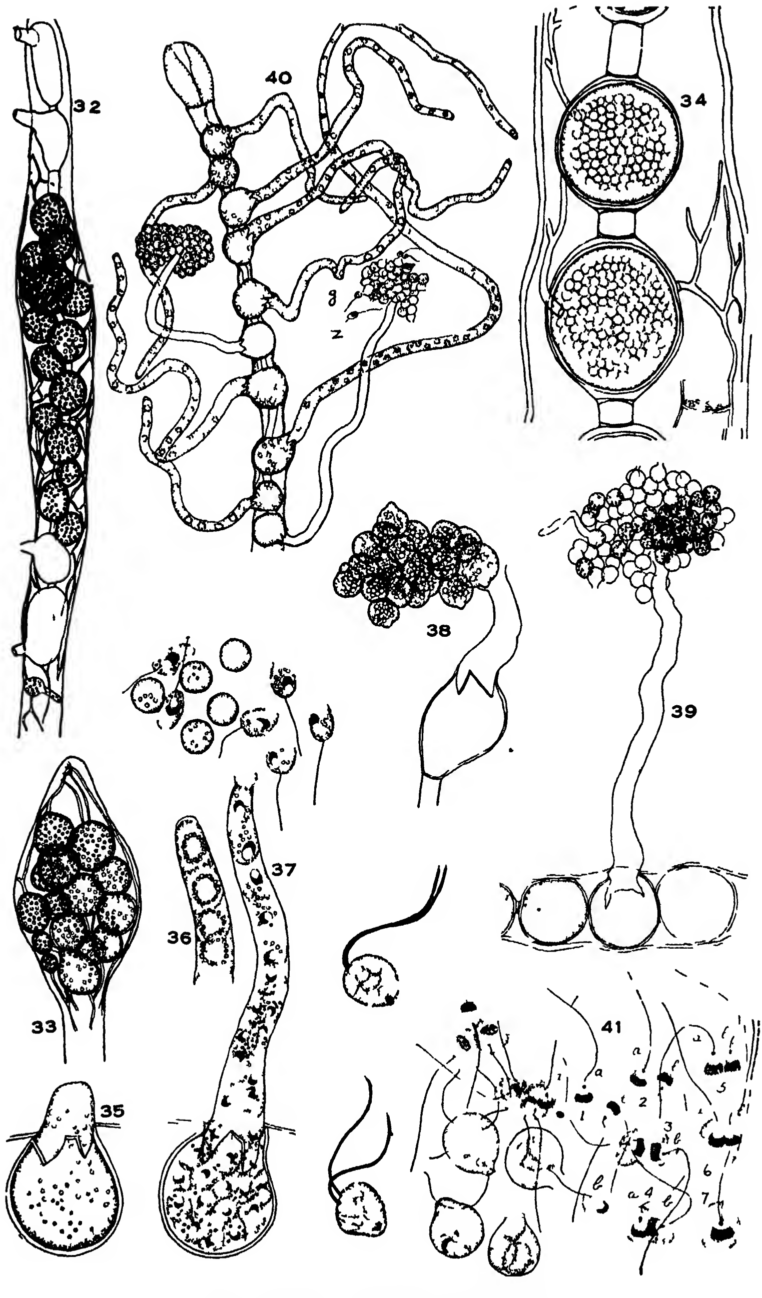
Zoospores were killed in a drop of water on a slide by exposure in a closed chamber to the fumes of 1 per cent osmic acid and stained immediately by stirring into the drop a small amount of freshly prepared aqueous solution of crystal violet. Such preparations may be studied immediately and show the whiplash cilium, the nucleus and nuclear cap, the side body apparently attached at one end to the base of the cilium, and the several fat bodies (FIG. 31). Gametes and zygotes (FIG. 42) have been stained in the same way.

Resting bodies appear as the host becomes exhausted. Their early development is as in the zoosporangia. Indeed in maturing cultures it is difficult to determine if a swelling is going to form a zoosporangium or resting body, until the papilla begins to form or the resting body wall begins to thicken. In a few instances, resting bodies have formed in zoosporangia which had developed papilla. When the resting body is formed, it shrinks slightly from the zoosporangial wall and then forms about itself a thick outer wall and a thin inner membrane (FIG. 34). The germination of the resting bodies has already been described.

Catenaria Allomycis, sp. nov.

In hyphis *Allomycis* et *Blastocladiellae simplicis* parasitica. Hyphae ramosae vel simplices, catenulatae cum rhizoideis paucis brevibus; hyphae 300–600 μ longitudine, ex zoosporangiis vel sporangiis perdurantibus catenulatim conjunctis per angustos isthmos compositae. Sporangia globosa vel oblongo-elliptica, 15–30 × 30–55 μ; zoosporae ovoideae, 5–6.3 × 6.3–7 μ. Cellulae perdurantes fulvosae vel leniter rubellae, globosae vel subglobosae, pariete levi vel minute punctato; siccatae germinantes per rimas irregulares parietis externi crassi; tubulo exeunte 50 ad aliquot 100 μ longitudine. Zoosporae ex cellulis perdurantibus uniflagellatae tempore dimissionis, prope tubulum exeuntem in irregulari cumulo in sporas immotas mox se convertentes. Sporae immotae sphericae, 5.4–6.4 μ diametro, post temporis spatium breve germinates et quattuor uniflagellatas cellulas sexuales formantes quae emergunt et per paria copulant. Cellulae sexuales 3 × 4.4–4.7 μ. Zygosporae biflagellatae, 3.5 × 7.6 μ, germinantes et hospitem penetrantes formantes thallum qui zoosporangia gignit.

Thallus parasitic in the threads of *Allomyces* and *Blastocladiella;* consisting when mature of a simple or branched catenulate hypha with a few stubby rhizoids; usually 300–600 μ long, consisting of 6–15 zoosporangia or resting bodies or both, sometimes much



FIGS. 32–41. *Catenaria Allomycis.*

longer and at times much shorter, being composed of only one zoosporangium or resting body; the swellings in the thallus connected by one-celled very rarely 2-celled short isthmuses, 5–9.2 × 7–16 μ. Septations incompletely formed, bumpy, pitted, or ridged. The first developed thalli forming zoosporangia, the later ones zoosporangia and resting bodies, and the last thalli only resting bodies. Zoosporangial development much as in *Allomyces* or *Blastocladiella simplex*. Zoospores with numerous fat bodies or lipoid granules, a conspicuous nuclear cap and a side body (visible only when stained), posteriorly uniflagellate. First zoospores emerging in a gelatinous envelope, the later ones emerging and swimming away upon reaching the exit; swimming smoothly as in *Blastocladiella*. Zoosporangia globose, subglobose, or pyriform to long elliptic or oblong elliptic, usually oval or ovoid; 15–30 × 30–55 μ; emergence tube 5–6 μ thick × 10–100 μ long. Zoospores oval, 5–6.3 × 6.3–7 μ, cilium about 17 μ long and tail piece 6.3 μ long. Resting bodies pale brown to pinkish; usually globose or subglobose, ovoid, elliptic, pyriform, rarely somewhat irregular in shape. On *Allomyces anomalus* 16–51 μ when globose, 30–41 × 34–42 when subglobose; on *A. javanicus* considerably larger, up to 63 μ thick when globose; wall of resting body 1–3 μ thick, smooth or very minutely rough; the whole spore surrounded by a thin-walled case which it almost completely fills. Resting body germinating by irregular cracking of the outer thick wall and the emergence of a germ tube which varies from 50–several hundred μ in length. Resting body zoospores uniciliate when discharged and capable of a little feeble movement, encysting almost immediately near the emergence pore in an irregular mass. Cysts spherical, 5.4–6.4 μ thick. After a rest period of about 2 hours germinating to form four uniciliate gametes which emerge through a pore to fuse in pairs, gametes 3 × 4.4–4.7 μ. Zygotes biciliate, 3.5–7.6 μ. Germinating and penetrating the host to form a zoosporangial thallus.

Found only once on *Allomyces anomalus* in soil collected by J. N. and Philip Couch from Texas, January 2, 1942.

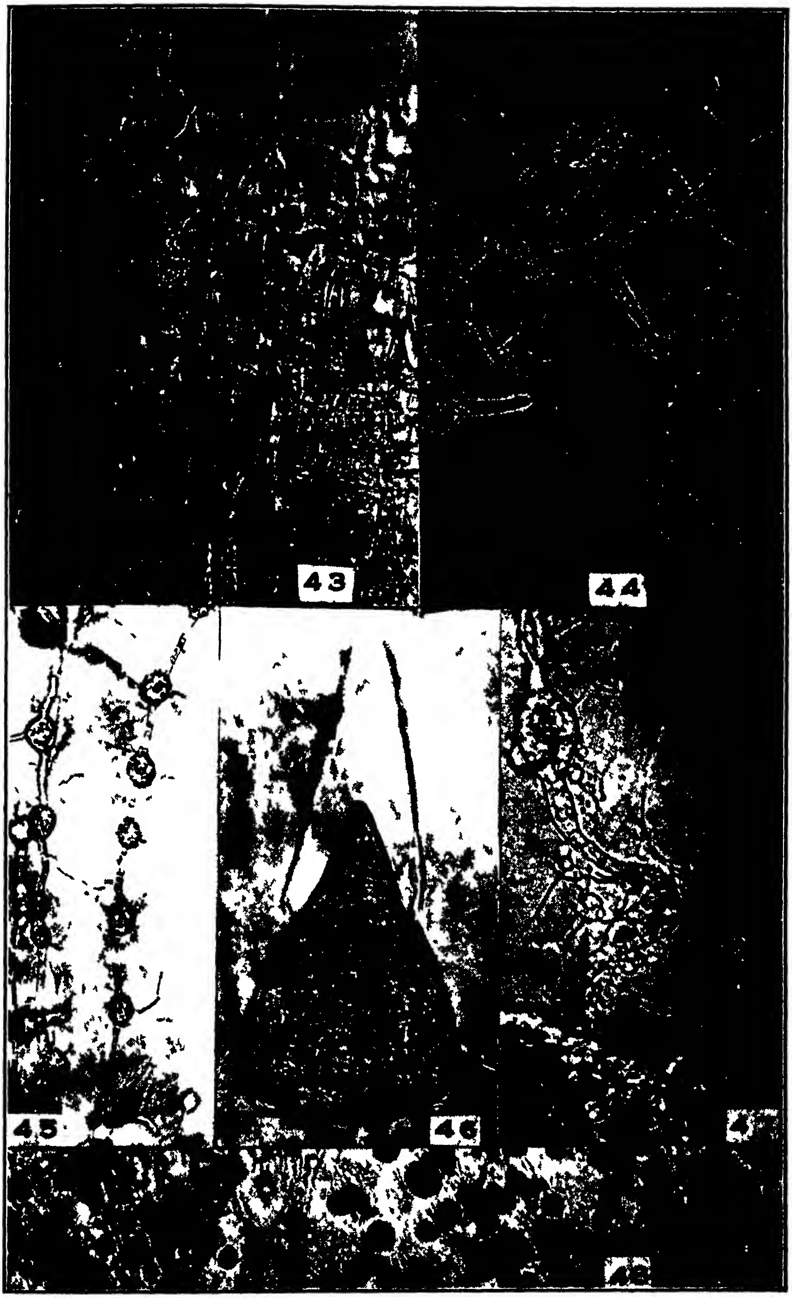
In its life cycle the above fungus shows a striking parallel to that of *Allomyces cystogenus* while in thallus structure it resembles *Catenaria Anguillulae*.

OBSERVATIONS ON CATENARIA ANGUILLULAE SOROKINE

According to the figures of Buckley and Clapham (1929) the resting body membrane of *Catenaria Anguillulae* cracks in germinating in the same distinctive manner as it does in the fungus

from Texas and in *Blastocladiella cystogena.* It seemed possible that *Catenaria Anguillulae,* which has heretofore been classified in the Chytridiales, might be more closely related to the Blastocladiales. It was imperative, therefore, that *C. Anguillulae* be studied again and compared with the fungus parasitic on *Allomyces anomalus.*

An intensive search was started for *Catenaria Anguillulae.* Sorokine and others had reported it on nematodes in Europe and Karling (**1934**) in this country had reported it on the roots of cooked grass, onions, several cooked algae and on the sterilized eggs of rotifers, infusoria and insects from New York City. Several collections of nematodes both free living and the species causing root knot of tomato were made and kept in wet soil from cow pastures but none of the nematodes were found parasitized by *Catenaria.* Boiled onion roots, which Karling (**1934**) found to be exceptionally favorable as a substratum for *C. Anguillulae,* were put in wet soil from local cow pastures, but the desired fungus failed to grow. Butler, J. B. and Buckley (**1927**) found *C. Anguillulae* on the eggs of the sheep liver fluke, *Fasciola hepatica,* in Ireland. They were unable to ascertain the source of infection, but suspected the fungus to be present in tap water from the Dublin water supply, in which the eggs were kept for several months. It would seem, if the *Catenaria* were a common parasite of the sheep fluke eggs, that it should occur in sheep pastures where sheep were infected. To test this hypothesis Dr. J. Wilford Olsen of Angleton, Texas, sent me fluke eggs and soil from a sheep pasture in that state, and Dr. J. N. Shaw of Corvallis, Oregon, sent similar material from Oregon. A tablespoonful of the Texas soil was put into each of six Petri dishes. The soil was banked to one side of the dish, leaving the other side clear, and sterile water was added to the dish. Fluke eggs from Texas were added to the clear side of each dish. Upon examination after two weeks, many of the fluke eggs in each of the six dishes were parasitized by *Catenaria Anguillulae,* and some were parasitized by *Rhizophydium* sp. The soil from Oregon treated similarly, yielded *Hyphochytrium catenoides* Karling, growing within many of the fluke eggs, but so far no *C. Anguillulae* has appeared.



FIGS. 43–48. *Catenaria Anguillulae.*

Catenaria Anguillulae was isolated in absolutely pure culture in the following way. Several infected fluke eggs were sucked up in a small pipet and dropped on a 2 per cent plain agar plate. Using a small needle sharpened to a chisel shape, each infected egg was dragged and pushed about under the binocular dissecting microscope over the agar, until it appeared to be free from bacteria and adhering trash. A block of agar with a single egg was then cut out under the binocular and transferred to agar F_{13}. Several eggs were so isolated, but the fungus grew from only a few. From such a growth several single threads were cut out and each thread transferred to a fresh plate of agar F_{13}. Several of these threads grew, but so slowly that the growth barely kept ahead of the bacteria. However, by cutting threads from the margin, it was possible to establish absolutely pure cultures on agar F_{13}. On this agar growth was slow, a culture attaining a diameter of 2 cms. after 30 days. It seemed desirable therefore, to look for a more favorable culture medium than agar F_{13}.

J. B. Butler and Humphries (1932) were the first to grow this fungus in artificial culture. Their best results were obtained in hanging drop preparations, where equal parts of a 0.25 per cent solution of agar in water, a concentrated fluke ova extract in water, and water were used as a growth medium. In this liquid medium with the growth still attached to a fluke egg, a culture about 1 mm. in diameter was obtained (Butler & Humphries, l. c. *pl. 15, fig. 15*).

It occurred to the writer that we might omit the fluke stage entirely and culture the fungus using liver as the source of nourishment. Since no sheep livers were available in the Chapel Hill market, beef liver was used instead. Preliminary tests with beef liver extract agar gave excellent growth. Beef liver agars with and without various sugars were next prepared as follows: a slice of liver (130 gms.) was chopped into small pieces with a razor and put in a towel and ground with a pestle in a mortar. A pinkish purple fluid was squeezed out and water was added to the liver in the towel and this was squeezed through until about 100 cc. of thick liver extract was obtained. Water filtered through blood charcoal was added to the liver extract to make 140 cc. This was boiled for about ten minutes until the proteins coagulated, strained

through a towel, and then divided into seven lots in flasks to which agar and sugars as indicated below were added:

L1—200 cc. liver extract, 1.5 per cent agar—no sugar
L2—200 cc. liver extract, 1.5 per cent agar— 2 grms. maltose
L3—200 cc. liver extract, 1.5 per cent agar— 2 grms. dextrose
L4—200 cc. liver extract, 1.5 per cent agar— 2 grms. sucrose
L5—200 cc. liver extract, 1.5 per cent agar— 2 grms. lactose
L6—200 cc. liver extract, 1.5 per cent agar—10 grms. liver paste
L7—200 cc. liver extract, 1.5 per cent agar—20 grms. liver paste

Petri dishes containing the seven different media were inoculated on the side of the dish. The best growth was obtained on the liver agar without any sugar, but with liver paste added (L7). In this medium the fungus covered the petri dish after about eight weeks, forming a very dense and compact, pale brownish growth, with many sporangia and resting bodies. The stronger the concentration of liver paste, the denser the growth; however, the mycelium spreads more rapidly over the dish in less concentrated liver extract media, but the growth is thin and relatively few reproductive bodies are formed. Of the sugars tested, the only one that promoted abundant growth was sucrose. On this (L4) growth was almost as good as on L6. The growth started slowly, but after about two weeks, the weekly increment was as great as on L7. On liver agar with the other sugars, dextrose, lactose, and maltose, growth was very slow, attaining less than a cm. diameter after eight weeks. However, the growth was very dense and compact. The liver agar is troublesome to prepare and hence I am using a 0.3 per cent meat extract (Difco) in 1.5 per cent agar for stock cultures.

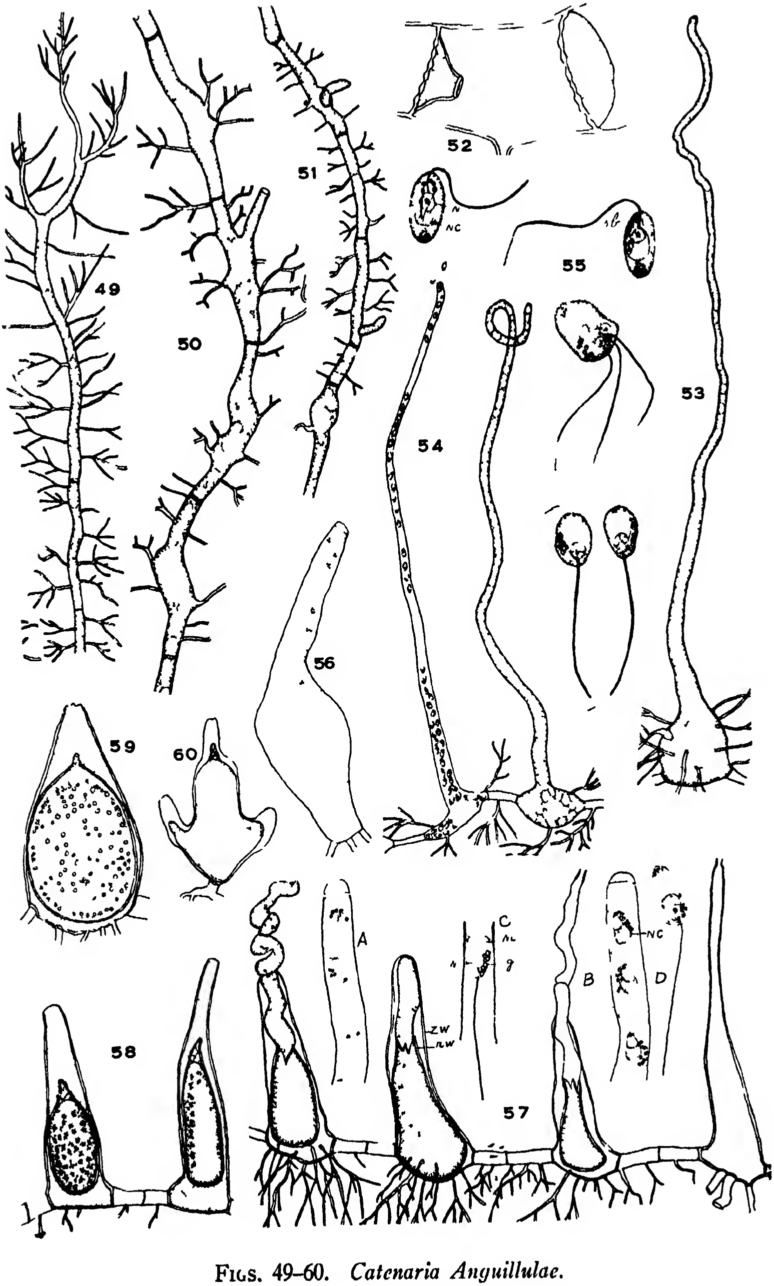
With the fungus in pure culture on agar it was possible to test its ability to grow on various kinds of substrata. However, because of the very extensive food range tests made by Karling (**1934**), it seemed necessary only to test the ability of our strain to grow on nematodes and on plant material. Free living nematodes, collected from branch water were cultured on F_{13} agar. To test the ability of the fungus to infect the nematodes, they were scraped from the surface of the agar and put in water in a Petri dish with zoosporangia and resting bodies of *Catenaria*. Nematodes causing the root knot of the tomato were tested at the same time. The *Catenaria* was able to parasitize both types of nema-

todes (FIGS. 63, 64). The plant material tested was cooked paspalum grass leaves in which the fungus grew, forming both zoosporangia and resting bodies (FIGS. 65–67).

DEVELOPMENT OF THE FUNGUS ON AGAR

The infection stages, the development of the thallus, and the formation of zoosporangia in the liver fluke eggs have been described in detail by Butler, J. B. and Buckley (**1927**). My observations on the development of the fungus in the fluke eggs corroborates theirs. Since the fluke eggs are opaque and the mycelium within them contorted, clear liver agar (as L1) furnishes a far better medium for the observation of the developing fungus. Hence, the observations to follow are made from agar cultures.

The growing end of a hypha tapers to a diameter of about 1 μ (FIG. 49). The rhizoids arise 2–100 μ back of the tip as minute stubs and grow out and branch about through the medium for a distance of a hundred or more microns. The rhizoids are 1–4 μ thick at the base but taper gradually to a fraction of a μ in thickness, retaining always a tubular aspect as indicated by E. J. Butler (**1928**), and by Hillegas (**1940**). The hyphal contents consist of rather coarsely granular, distinctly vacuolate protoplasm. In the growing region, there are no septations, but some distance back from the tip, where the hyphae have attained their mature thickness, septations appear. These are few at first and spaced at irregular intervals. As the hyphae mature, they become more or less regularly septate, the spaces between the cross walls varying from about 60–130 μ long. The swellings which will form the sporangia may start to enlarge either before or after the regular septations are laid down (FIGS. 49–51). Sorokine (**1876**) states, and his figures show, that the septations appear before the swellings, while this is contradicted by Dangeard (**1885**). Butler (**1928**) agrees with Dangeard, stating that the septations are formed after the swellings. Both of these observations are partly correct, since the septations appear both before and after the swellings, but are not so abundant before the swellings as figured by Sorokine. As the swellings are formed, the protoplasm flows into them from both sides until the hypha becomes nearly empty except for the inter-

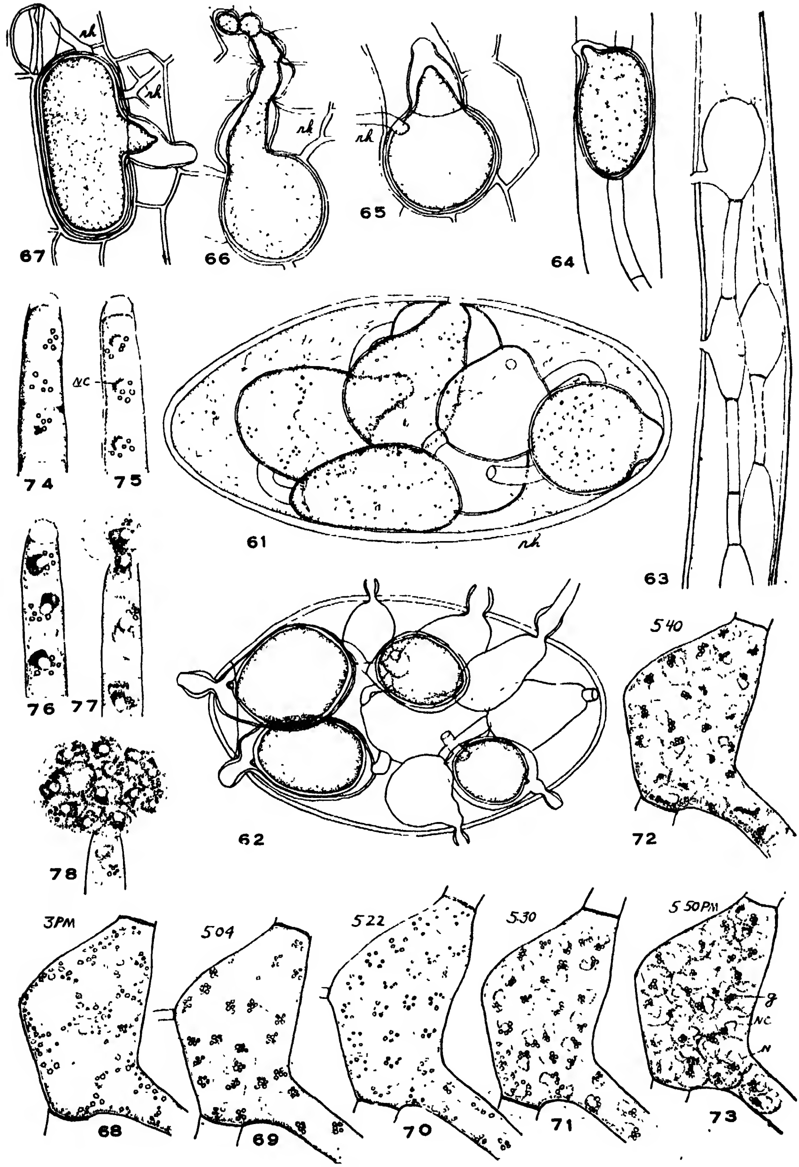


FIGS. 49–60. *Catenaria Anguillulae.*

calary swellings. Cross walls are now formed separating the swollen parts from the unswollen. The swellings become the zoosporangia or resting sporangia, connected by the hyphal isthmuses. These may be once septate or non-septate, depending upon whether the hyphae become septate or not, before the swellings start to form. Sorokine says that the isthmuses are two-celled, *i.e.* once septate, but his figures show them both septate and non-septate.

The development of the sporangium from the time it begins to swell until it attains mature size has not been followed in detail either by previous observers or by me. The observations reported here begin when the sporangium has reached mature size, and end with spore emergence. When mature in size, the cytoplasm contains a large number of spherical vacuoles of variable size and many fat (?) bodies, some of which are 2 or 3 microns thick, but most of which are about 1 μ thick (FIG. 68). While the sporangium is still in the vacuolate stage, the fat globules become arranged in groups of fours or fives and become associated with a rounded body which may be the nucleus (FIG. 69). The clusters are about evenly spaced from each other, and each cluster will be the center of a zoospore and may at this stage show a slight rocking motion.

The vacuoles disappear rather suddenly and though they are for the most part large and conspicuous, I am still uncertain about their fate. By concentrating observations on one large vacuole, something has been learned. The outline became irregular and vague and in a few seconds had disappeared. All vacuoles disappeared almost simultaneously, and immediately cleavage furrows became evident, the furrows apparently forming from the material contained within the vacuoles (FIG. 70). If this were so, it would furnish evidence that the vacuolar material was cytoplasmic in nature and hence living, and that the cleavage process was not an osmotic or turgor process alone, but one involving the rearrangement and redistribution of the vacuolar material in between the spore origins. In fifteen to twenty minutes after the vacuoles disappeared, the contents of the sporangium were divided into polygonal areas, each a spore origin with a cluster of 4 to 8 globules (FIG. 70). After about thirty minutes, the cleavage furrows between the spore origins disappeared and soon a greenish hyaline material began to take on a half-moon shape on one side of the nu-



FIGS. 61–78. *Catenaria Anguillulae.*

cleus (FIG. 71). This is the nuclear cap. The spores now re-formed and became polygonal again (FIG. 72). While in this shape the spores showed considerable motion. A single spore might spin around, but retained its polygonal shape and position in the sporangium. Shortly before emerging, *i.e.* two or three minutes, the spores became round and began a rocking and trembling motion (FIG. 73).

Meanwhile changes had taken place in the wall substance of the tip of the emergence papilla. This thickened until it took on the appearance of a convex lid (FIG. 74). A few minutes before spore discharge, this region gelatinized, the gelatinous material pushing backward in the tube, forcing the spores back (FIGS. 75, 76). In several instances the outer part of the gelatinizing tip broke away as a fairly distinct lid. Suddenly the gelatine expanded outwards into a spherical, hyaline ball, the spores now moving outwards as though pushed by some expanding, intersporal substance (FIG. 77). The first spore pushed out into the center of this hyaline sphere and others followed rapidly to form a spherical ball of spores (FIGS. 77, 78). At first the spores were quiet, but in a few seconds they became active; the envelope burst and the spores which were in the ball swam away. The remaining spores emerged singly and swam away as they reached the exterior. While it seems the rule for the first spores to be discharged into a spherical mass surrounded by hyaline material, this is by no means always the case, for often the tip gives way and the first as well as the later spores swim away upon reaching the exterior. Sometimes the first spores to emerge may collect into an irregular mass, swimming away one by one as they become disentangled. Thus in perfectly normal and uninjured material one may find at different times all the variations in spore discharge which have been described by Sorokine, Dangeard, and others, except that in no instance have I observed spores discharged without cilia. The above observations confirm those of Dangeard (1885) and Karling (1938). One interesting variation noted by Karling (1938) related to the discharge of multiciliated masses of protoplasm from the zoosporangia. As observed by him, these may swim about in uncoordinated fashion or they may creep about like an amoeba. Some of these masses absorbed water and swelled to more than a hundred microns in diameter. On

such monsters the ends of some of the cilia became swollen to form a vesicle. This is excellent evidence that the cilium is a tubular structure with a core of perhaps vacuolar material. Structures which look like vesicles have been referred to by Berdan (**1941**) as loops. The zoospores as in *Catenaria Allomycis* have the structure (FIGS. 47, 55) and method of swimming characteristic of the Blastocladiales.

VALIDITY OF SPECIES OF CATENARIA

The fungi which have been described under the name of *Catenaria Anguillulae* certainly represent more than one species, as has been suggested by several authors and probably do not all even belong to the same genus or family. Indeed it is impossible to be certain as to Sorokine's type, since it was inadequately and perhaps partly incorrectly described. On the other hand, it seems highly likely that the fungi identified by Dangeard (**1885**), Constantineau (**1901**), J. B. Butler and Buckley (**1927**), E. J. Butler (**1928**), Buckley and Clapham (**1929**), J. B. Butler and Humphries (**1932**), and Karling (**1934**) as *Catenaria Anguillulae* are all one and the same species and identical with the species described here. It has been pointed out by Dangeard and others that the chief apparent differences between Sorokine's fungus and theirs is in the abundance of rhizoids, and the smaller dimensions of the sporangia and zoospores in Sorokine's fungus. I was able to infect nematodes with inoculum from a pure culture of my strain of *C. Anguillulae* (FIGS. 63, 64). On the nematodes my fungus agreed remarkably well with Sorokine's. It is easy to understand how Sorokine might have overlooked the rhizoids with a magnification of 450 diameters, for I find they are difficult to see in a nematode even with a 70 × water immersion objective. Sorokine gives the sporangia as 8–10 × 10–17 μ and the spores as 1.5–2 μ thick. It is possible, indeed likely, that these figures are wrong, for if one calculates the size of the sporangia and spores from Sorokine's drawings, the sporangia are 10–26 × 20–53 μ, the largest one shown (Sorokine, l. c. FIG. 24, sporangium to right) is 26 × 53 μ; the zoospores are about 4 × 6 μ. Sorokine incorrectly describes the cilia as forming after the spores emerged, and states that the spores

have a single, conspicuous globule which he calls a nucleus. These are doubtless errors of observation due to the low magnification used. He correctly notes that the movement of the spores of *Catenaria* does not resemble that of the spores of the chytrids. Sorokine says that the spores emerge one by one or by twos, threes, or indeed they may emerge in a mass separating immediately after their exit to swim away. After the sporangium becomes partly empty, the spores remaining in the sporangium begin moving about.

Dangeard (**1885**) first suggested that the organism described by Villot (**1874**) as a fresh water alga parasitic on the hair worm, Gordius, was in reality the fungus *Catenaria Anguillulae*. Villot was of the opinion that more than one species of fresh water alga [*Catenaria*] was involved. On pages 181 and 182 Villot describes the methods used in studying the structure of the hair-worms. Free hand sections were made of fresh worms and the sections were cleared in a mixture of acetic acid, 1; alcohol, 1; glycerine, 1; distilled water, 2. Staining with carmine was found useful. It was apparently in material so treated that the fungus was observed. Such treatment probably accounts for the collapse of the contents of the sporangia in figure 13. Villot states that the zoospores are spherical, 2 μ thick and without cilia. He says that the spores occur in great numbers in suspension in the water of the streams. It is very likely that Villot had the spores of some other organism. In figure 14, he shows what he calls a zoosporangium. This is undoubtedly a typical resting body, so well drawn that it shows the characteristic papilla shown by Buckley and Clapham (**1929**) and myself. Indeed I regard this resting body as the best evidence that Villot's fungus belonged to the genus *Catenaria*. Villot gives the diameter of the hyphae as 2 μ thick, which is about half the diameter of the smallest hyphae I have seen. The thickest isthmus shown in figure 13 is slightly more than 4 μ thick; those in figures 14 and 16, 2.5 and 2 μ thick respectively. The largest sporangia shown, figure 16, are about 15 × 25 μ which agree well with the sizes of Sorokine's, according to my calculations.

Karling (**1934, 1938**) showed that *C. Anguillulae* would grow on a very wide range of plant and animal material. The strain reported on in this paper grows on nematodes, fluke eggs, and

various other substrata. I hope to try it on Gordius when I can find such worms. Until this is done, we must remain in doubt as to the specific identity of Villot's fungus.

The fungus described and illustrated by Sparrow (1932) as *C. Anguillulae* is certainly not the same as *C. Anguillulae* in the sense of Dangeard and as interpreted here. The spores of Sparrow's fungus were 2 μ in diameter, spherical, and with one or two oil globules. If the spore is correctly described, this fungus would hardly seem to belong to the genus *Catenaria*. It must be regarded as a fungus whose relationship is doubtful.

Karling (1942, p. 622) reported the resting bodies of *C. Anguillulae* in material collected in Cypress Gardens, South Carolina. He states that they are spherical, oval, oblong, and full of yellowish-amber, refractive material, and have a fairly thick, hyaline wall. In my material, the wall of the resting body is pale brown in color and the contents hyaline. Even when the main part of the spore is spherical, it always has a short papilla or "pip" on its surface beneath the old empty tube. Since Karling does not mention this very characteristic pip, and the color of the resting bodies mentioned by him does not correspond with that of *C. Anguillulae*, it is doubtful if the resting bodies from South Carolina belong to *C. Anguillulae* as interpreted here.

Serbinow's *Catenaria pygmaea* has been regarded as a doubtful species of *Catenaria* by von Minden (1911), E. J. Butler (1928), and others. In this species the thallus is monocentric, the zoospores 1.5 μ thick, with a single fat body, and the resting bodies are spherical, having a smooth colorless membrane with a central fat body, characters which should certainly exclude Serbinow's species from the genus.

Karling's (1928) *Catenaria sphaerocarpa* is distinguished primarily by the spherical zoospores with a single conspicuous refractive globule, the zoospores swimming as in the monocentric chytrids; by the usually spherical resting spores with a thick brown wall, and the predominantly spherical zoosporangia. The structure of the zoospores is of such basic and fundamental importance in determining relationships that on this character alone *C. sphaerocarpa* should not be included in *Catenaria* as interpreted here.

We are thus left with only one species in the genus *Catenaria*, *C. Anguillulae* in the sense of Dangeard, the two Butlers, Buckley and Clapham and others (see p. above). As pointed out above, we can never know for certain if Sorokine's type is the same as the fungus described by Dangeard, Butler, and others, unless someone can rediscover Sorokine's fungus from the type locality. However, I think the evidence is in favor of the view that Sorokine's and Villot's fungi belong in the same genus with Dangeard's and mine. Whether or not all three are the same species can only be determined with certainty by further study of the parasites of Gordius and eel-worms. For the present, I think it prudent to follow a suggestion made by Karling (1938) and to retain the name *C. Anguillulae* for the fungi studied by Villot, Sorokine, Dangeard, Constantineau, J. B. Butler and Buckley, E. J. Butler, Buckley and Clapham, Butler and Humphries, Karling, and myself.

The following description drawn up from the material from Texas, allows sufficient latitude for the inclusion of all the above forms, if one makes sufficient allowance for the measurements of Villot and Sorokine and some of the perhaps faulty observations of the latter.

CATENARIA ANGUILLULAE Sorokine.

Parasitic or saprophytic in nematodes, liver fluke eggs, and saprophytic on cooked grass leaves, etc., and various kinds of nutrient agar. Thallus composed at first of a branched or unbranched nonseptate or sparingly septate hypha, with rhizoids. Hypha 4–15 μ thick, swelling at more or less regular intervals to form zoosporangia or resting bodies connected by narrow one or two celled isthmuses and thus catenulate. Zoosporangia pyriform or subpyriform in fluke eggs, 25–36 × 38–71 μ or considerably smaller when crowded, emergence papillae 5–8.6 × 8–several hundred microns long, connecting isthmuses 5–5.4 × 4–14 μ; in nematodes zoosporangia oval or elliptic, 9–20 × 12–34 μ, the emergence papilla only projecting through the nematode skin; on liver agar zoosporangia subglobose with very long emergence tubes, up to a mm. long; zoospores completely formed within the sporangium, usually showing rocking motion before discharge; first spores usually emerging to form a spherical mass enclosed by a gelatinous substance at the tip; this gelatinous envelope soon dissolves and the first spores swim away, the rest of the spores swim away as soon as they reach the exit, or first spores may swim away im-

mediately; zoospores 3.8–5.4 × 6.7–8 μ, tapering toward the anterior end, with 3–4 anterior fat (?) globules, a distinct nuclear cap and nucleus to one side of which is a side body and several fat? globules; with one posterior whiplash cilium; rounding up and encysting before germinating, 4.6–5.4 μ; germinating in water or nutrient agar by sending out a delicate rhizoid and then forming a tubular growth from the opposite pole, which may form a dwarf sporangium with a small, sterile basal part, or may grow into a new mycelium if sufficient food is available [on fluke eggs, zoospore leaves empty cyst on outside of egg membrane (Butler & Buckley, **1927**)]. Resting bodies formed on nematodes, fluke eggs, leaf tissue, and nutrient agars; formed within zoosporangial membrane and conforming somewhat to its shape, resting spore protoplasm retreating from the old sporangial wall and forming a new thick pale brownish wall of its own; on nematodes oval or oblong ovate, 16–18 × 20–33 μ, in fluke eggs spherical, subspherical, ovoid or irregular in shape, 21–42 μ when spherical, 20–33 × 40–55 μ when subspherical; on boiled leaves spherical, pyriform, lobed, or cylindrical with rounded ends frequently conforming to the leaf cells except for a cone-shaped part through which the emergence tube sprouts, 30–50 × 38–100 μ; on agar spherical or subspherical, except for a small or large cone-shaped elongation up to over 100 μ long, on agar No. 5 up to 138–176 μ thick when spherical or subspherical; wall smooth except for a short papilla apparently always present and always directed towards emergence pore of zoosporangium, wall about 2–3 μ thick. Resting sporangium germinating by the irregular cracking of the outer thicker wall and the emergence of a long or short tube through which the zoospores emerge as in the zoosporangium. Zoospores in resting sporangia as in zoosporangia.

Isolated by the writer from sheep liver-fluke eggs from Texas, which were put in wet soil collected from a sheep pasture near Angleton, Texas, May, 1944. Soil and fluke eggs collected by Dr. J. Wilford Olsen, May, 1944.

Sparrow (**1943**) recognized the Catenarioideae as a subfamily in the Chytridiales. In view of the studies presented here it seems advisable to transfer the genus to the Blastocladiales as a family.

Catenariaceae fam. nov.

(Subfam. Catenarioideae Sparrow)

Fungi in vermibus et in aliis fungis parasitici, vel in materia plantarum et animalium saprophytici. Thallus immaturus tubulatus, maturus catenulatus

cum rhizoideis paucis vel numerosis. Zoosporae omnibus rebus similes illis Blastocladialium. Cellulae perdurantes ut in Blastocladialibus efformatae, pariete levi vel minute punctato fulvoso; protoplasmate hyalino. Zoosporae ex cellulis perdurantibus pusillos thallos gignentes aut in sporas immotas (gametangia) se convertentes et quattuor cellulas sexuales formantes quae per paria copulant et biflagellatas zygosporas formant.

Parasitic on worms, other fungi or saprophytic on a great variety of plant and animal substrata. Thallus worm-like, unbranched or sparingly branched, with a few to many rhizoids, swelling at more or less regular intervals to form the reproductive organs which are zoosporangia or resting bodies connected by one or two-celled narrow isthmuses. Zoospore formation, discharge, and structure as in the Blastocladiales. Resting bodies formed within the zoosporangial or hyphal membrane usually contracting from the membrane to leave a more or less conspicuous space. Wall of resting body smooth or very minutely pitted or with a single pip, pale brown, contents hyaline. In germinating the resting body is transformed into a sporangium, the outer wall cracks irregularly and through this crack a tube of variable length emerges. Zoospores from resting bodies uniciliate and acting as zoospores which give rise to dwarf thalli or encysting and acting as gametangia to form four gametes which fuse in pairs to form a biciliate zygote.

What is the justification for the transference of *Catenaria* from the Chytridiales to the Blastocladiales? Sorokine (**1876**) suggested that *Catenaria* resembled *Achlyogeton* in its development. Dangeard (**1885**) placed it tentatively in the Ancylistales, but Fischer (**1892**), Schröter (**1897**), von Minden (**1911**), Fitzpatrick (**1930**), Karling (**1932**), Sparrow (**1943**), Whiffen (**1944**) have put it in the polycentric Chytridiales. Sparrow (**1943**), recognizing the peculiar thallus of *Catenaria* when compared with the chytrids, put the genus in a subfamily, the *Catenarioideae*. Karling (**1931**) in his review of *Catenaria* points out that the method of formation of the resting bodies is quite unlike that of other species of the *Cladochytriaceae* and follows Dangeard in suggesting a possible relationship to the Ancylistales.

The reasons for putting *Catenaria* in the Blastocladiales may be summarized as follows:

1. The zoospore structure is similar to the structure of the spores in the Blastocladiales, with numerous fat bodies, a side body, and a nuclear cap.

2. Zoospore discharge is typical of the Blastocladiales, *i.e.* the first zoospores to emerge collect in a ball at the sporangial tip as in *Blastocladiella*, *Allomyces*, etc.

3. The zoospore swims as in the Blastocladiales.

4. Zoospore germination is usually as in the Blastocladiales, *i.e.* bipolar instead of monopolar. First noted by Dangeard, 1885.

5. The resting body is formed in a hyphal or zoosporangial case as in the Blastocladiales, and germinates as in that order and not as in any chytrid.

6. Septations are frequently irregular, *i.e.* bumpy, ridged or apparently pitted.

7. Life cycles parallel certain Blastocladiales. *Catenaria Anguillulae* has a life cycle as in *Allomyces anomalus* or *Blastocladiella simplex, laevisperma,* or *asperosperma; C. Allomycis* as in *Allomyces cystogenus.*

From the above it is clear that *Catenaria* is closer to the genera *Blastocladiella* and *Allomyces* than to any other fungi. Indeed one might consider *Catenaria* as a sort of polycentric *Blastocladiella* though I do not think either of these fungi arose from the other. The catenulate thallus is the chief basis justifying the establishment of a separate family, but in *Allomyces moniliformis* one frequently finds the zoosporangia and resting bodies connected by isthmuses as in *Catenaria* (FIG. 12).

SUMMARY

A fungus with a thallus similar to *Catenaria Anguillulae* and resting bodies that germinate as in *Blastocladiella cystogena* has been isolated from soil with its host, *Allomyces anomalus.* Growth experiments indicate that it is an obligate parasite on species of *Allomyces* and *Blastocladiella simplex.* It failed to grow on *B. cystogena, B. laevisperma,* or *B. asperosperma,* or on *Blastocladia parva, Achlya* sp. or *Saprolegnia* sp. Infection stages on *Allomyces anomalus,* the development of the thallus, zoosporangia, resting bodies, and the fusion of motile gametes are described. The fungus is named *Catenaria Allomycis. Catenaria Anguillulae* has been isolated from Texas soil and grown in pure culture on a variety of agars for the first time. It grows best on beef liver agar

with or without sucrose, on which it forms a much branched thallus with numerous rhizoids. It can be transferred to liver fluke eggs, adult nematodes, and boiled grass leaves. Zoosporangia are formed in nearly all culture media tried. Resting bodies are formed sparingly in liver fluke eggs, nematodes, grass leaves, but are formed abundantly in strong concentrations of liver agar. The resting bodies are formed and germinate much as in *Blastocladiella*. On the bases of zoospore structure, method of discharge, and swimming and resting body structure and germination, the genus *Catenaria* is transferred from the Chytridiales to the order Blastocladiales, and Sparrow's subfamily *Catenarioideae* is raised to family rank. The species *Catenaria Allomycis* shows a parallel in its life history to *Allomyces cystogenus* while the life cycle of *C. Anguillulae* is similar to that of *A. anomalus*.

UNIV. OF NORTH CAROLINA,
CHAPEL HILL, N. C.

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EXPLANATION OF FIGURES

FIGS. 1–11. *Catenaria Allomycis*. The host is *Allomyces anomalus*. 1, hypha of host with short half mature parasite, × 100; 2, heavily infected branched hypha showing spherical resting bodies and empty zoosporangia of parasite, × 100; 3, dichotomously branched hypha of parasite in host, × 100; 4, zoosporangia of host and nearly mature hypha of parasite, × 100; 5, two empty zoosporangia and resting bodies of parasite, note septations, × 100; 6, germinating resting bodies of parasite, note long tube on right and two loose clusters of cysts near center, × 150; 7, germinated resting body showing irregularly cracked wall, emergence tube, and several encysted resting-body zoospores, other zoospores are out of field, × 700; 8, empty cysts and one with two or three gametes, × 1400; 9, empty cysts and gametes emerging, × 1050; 10, zygote stained with two cilia separated, × 1400; 11, same with two cilia together, × 1400.

FIGS. 12–31. *Catenaria Allomycis*. Fig. 12, on *Allomyces moniliformis*, all others on *Allomyces anomalus*. 12, zoosporangia of *Allomyces moniliformis* showing connecting isthmuses, × 127; 13–20, stages in invasion of host by parasite, × 1244; 21–24, stages in development of parasite from small

oval body to the catenulate thallus with rhizoids and septations, × 564; 25, dwarf thallus forming single sporangium in exhausted host thread, × 675; 26–30, development and discharge of zoospores, see text for explanation, × 675; 31, zoospores killed and stained, drawn while wet; n.c., nuclear cap; n, nucleus; s.b., side body; g, lipoid granules or fat bodies, × 1244.

FIGS. 32–42. *Catenaria Allomycis.* Host *Allomyces anomalus.* 32, 33, habit sketches showing empty zoosporangia and resting sporangia in thread of *Allomyces,* × 235; 34, resting sporangia and rhizoids in thread of *Allomyces,* × 800, small insert lower right shows perforated septum of parasite, × 1120; 35, wall of resting sporangium cracked and germ tube growing out through crack and host wall, × 508; 36, distal part of tube of same resting sporangium, but later, showing r.s. zoospores forming, note distinct circles of fat bodies, × 508; 37, r.s. zoospores emerging, some swimming sluggishly, others encysted, × 508; 38, cysts with papillae formed, × 608; 39, cysts some empty at tip of emergence tube of resting sporangium, note one cyst (?) germinating by tube, × 294; 40, habit sketch of germinating resting bodies of *C. Allomycis* with extra long tubes, note distinct and very characteristic circles of fat globules, a "circle" for each spore, on left a cluster of cysts, on right gametes emerging from cysts, g, gamete, z, zygote, × 152; 41, emergence of gametes from cysts and fusion of gametes in living material, × 1120; 42, two zygotes, killed with fumes of osmic acid and stained with gentian violet, × 1120.

FIGS. 43–48. *Catenaria Anguillulae.* 43, vertical section through agar No. 5 showing resting bodies and zoosporangia, × 200; 44, in 0.3 per cent meat broth extract and then in charcoal water, zoosporangia and rhizoids, × 100; 45, on 0.3 per cent meat extract agar + 1 per cent dextrose, × 150; 46, resting body from agar No. 5, × 700; 47, on 0.3 per cent meat extract agar, note rhizoids have blunt tips, × 400; 48, on F_{13} agar, sector on right with resting bodies, on left without, × 100.

FIGS. 49–60. *Catenaria Anguillulae.* 49–51, hyphae on liver agar; 49, distal part of hypha showing 2 septations before swellings start; 50, septations separating swellings, end walls delimiting sporangia from isthmuses will form later; 51, sporangia forming with a minimum of swelling, × 224; 52, cross walls in hypha showing pits, × 1065; 53, 54, zoosporangia with long tubes, from culture in meat extract broth transferred to charcoal water, spores emerging in sporangium on left, × 137; 55, stained material showing four normal and 1 giant spore with 3 cilia, two lower spores dried over night, nuclear cap appeared as empty space, s.b., side body; n, nucleus; n.c., nuclear cap, × 1065; 56, dwarf zoosporangium in water cultures with boiled grass but not attached to it, × 577; 57, three resting sporangia in stage of germination and one empty zoosporangium on right, × 224; z.w., zoosporangial wall; r.w., resting sporangial wall, on L7 agar. Insert A, zoospores in tip of tube about 15–20 minutes before discharge, nucleus and fat bodies distinct, tip beginning to gelatinize; B, 15 minutes later nuclear cap (n.c.) formed, tip gelatinizing; C, spore emerging cilium trailing; D, diagram of spore in swimming condition, A–D, × 1065; 58, two resting sporangia on L7 agar, note cytoplasm between resting body and zoosporangial wall, × 224; 59, resting sporangium, on L3 agar, × 224; 60, lobed resting sporangium, on L3 agar, × 137.

FIGS. 61–78. *Catenaria Anguillulae* Sorokine. 61, 62, on liver fluke eggs from Texas in soil from Texas; 61, shows three immature zoosporangia and one immature resting sporangium, several empty zoosporangia, indistinct rhizoids and disintegrated contents of fluke egg, note emergence pore of zoosporangia; 62, several empty zoosporangia showing emergence tubes and four resting sporangia, × 445; 63, 64, on nematode sp.; 63, empty zoosporangia, × 445; 64, resting sporangium, × 445; 65–67, resting sporangia in boiled leaf, paspalum grass, × 280; 68–73, zoosporangial development, see text for explanation, n, nucleus; n.c., nuclear cap; g, fat globules, × 760; 74–78, distal part of zoosporangial tube, see text for explanation, × 1065.

NOTES ON THE CULTURE OF COPRINUS ASTEROPHORUS [1]

Horace L. Barnett

(with 7 figures)

In the spring of 1942, four fruit bodies of a species of *Coprinus* were collected in sandy soil by a roadside near Mesilla Park, New Mexico. The specimens were dried and stored in the laboratory. Interest in this brief study of this fungus was stimulated by Dr. W. H. Long, who saw the specimens and identified them as belonging to an unnamed species. It has recently been described and named *Coprinus asterophorus* Long and Miller.[2]

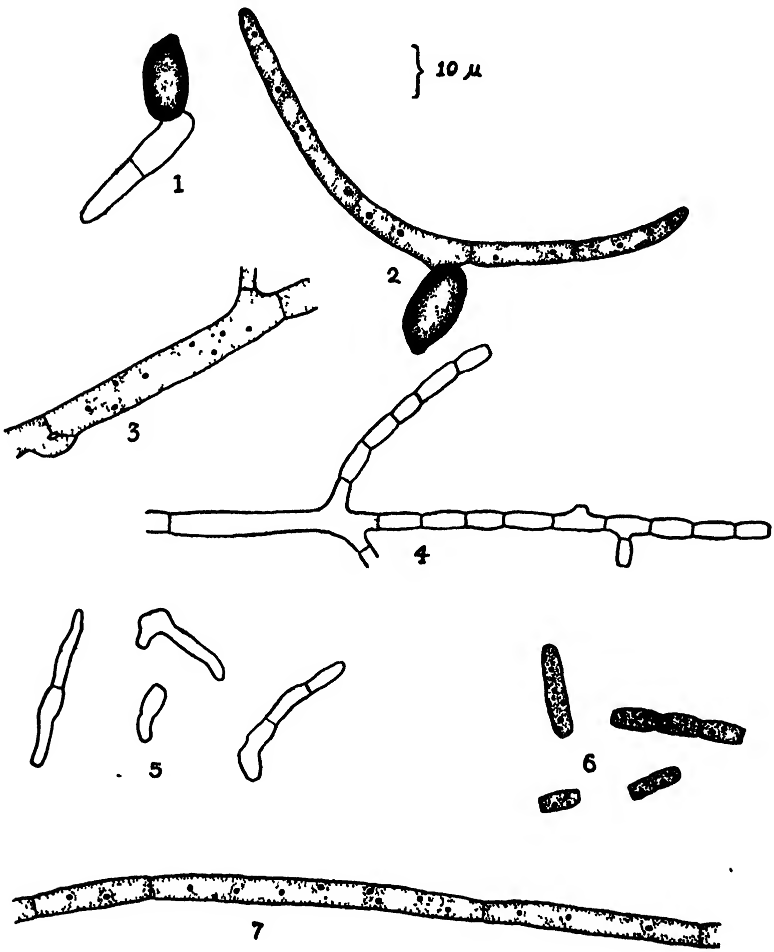
In the fall of 1942 the spores from a dried fruit body were sown on potato-dextrose agar plates. Germination was slow, beginning after 24 hours, with only a small percentage of the spores germinating. A single germ tube appears at the end opposite the apiculus (fig. 1) and soon branches, commonly forming a two-pronged structure (fig. 2). Soon, numerous branches are produced. No clamp connections are present on the young mycelium.

The growth of the mycelium at room temperature is fairly rapid. Macroscopically, the mycelium is pure white, much of it being aerial, and has a fluffy tufted appearance. After several days, microscopic examination revealed the presence of clamp connections on both the submerged and aerial portions of the mycelium (fig. 3), being more frequent on the latter, but not very abundant on either. Oidia were present on the aerial tufts. The oidia are formed by the segmentation of some of the upright hyphae (fig. 4). They are rod-shaped and range from 5 to 15 μ in length. On agar the oidia germinate by one or two germ tubes (fig. 5) and produce normal mycelium with clamp connections.

[1] The investigations on which this article is based were completed at New Mexico College of Agriculture and Mechanic Arts, State College, New Mexico.

[2] Long, W. H. & Vera Mentzer Miller. *Coprinus asterophorus*, a new desert *Coprinus*. Mycologia 37: 120. 1945.

Single germinated basidiospores were picked out with a needle and cultured. The resultant mycelia were, from all appearances, like those which arose from many spores. After 10 days, the cul-



FIGS. 1 and 2, basidiospores germinating on agar, 3, portion of older mycelium showing clamp connection and nuclei; 4, portion of aerial hypha showing the formation of oidia, 5, oidia germinating on agar; 6, oidia showing nuclei; 7, portion of mycelium showing cells with varied number of nuclei. Figs. 1, 4 and 5 are from unstained material.

tures were examined microscopically. All of the 17 single spore cultures obtained produced clamp connections and oidia. Thus, the species is homothallic.

All attempts to stimulate the production of fruit bodies in pure culture failed.

Germinated basidiospores and mycelium were stained with Heidenhain's Iron-alum Haematoxylin. As far as could be determined, the first cell of the germ tube is binucleate, although only a few germ tubes in this stage were observed. Since the spore wall is very dark and only mature spores were available, it could not be determined whether the basidiospore contains one or two nuclei.

The cells of the mycelium contain two or more nuclei (FIGS. 3, 7). This is true for mycelium resulting from a single spore as well as that resulting from many spores. The number of nuclei in one cell is more often even, but not constantly so. In general, the longer cells contained the larger number of nuclei.

Most of the oidia were found to contain either two or four nuclei (FIG. 6), although a few uninucleate oidia were seen. The binucleate condition seemed to be typical. Those containing four nuclei often appeared to break up into two binucleate oidia.

SUMMARY

Coprinus asterophorus is a homothallic species, producing clamp connections and typically binucleate oidia which germinate to produce typical mycelium with multinucleate or binucleate cells.

DEPARTMENT OF BOTANY,
STATE UNIVERSITY OF IOWA,
IOWA CITY, IOWA

THE GENUS LAMPRODERMA AND ITS RELATIONSHIPS. II

MARY LOUISE DENNISON

(WITH 1 FIGURE)

STEMONITACEAE

Spores in mass black, deep violaceous or ferruginous; capillitium always present; peridium and capillitium limeless; lime, if present, restricted to hypothallus, stipe and columella; fructifications aethalioid or of separate and distinct, globose to cylindric, sessile to stipitate sporangia; columella varying from almost none to very prominent; capillitium typically abundant, composed of rather slender, freely branching and anastomosing threads arising from the columella or base of the sporangium, the tips free, attached to the peridium or united to form a surface net; peridium evanescent to persistent.

In the Stemonitaceae as proposed the following genera will be included: *Schenella* (?), *Amaurochaete, Brefeldia, Diacheopsis, Diachea, Elaeomyxa, Macbrideola, Enerthenema, Clastoderma, Barbeyella, Lamproderma, Stemonitis,* and *Comatricha.*

Type Genus: *Stemonitis* Gleditsch emend. Rost.

KEY TO GENERA

a. Fructification aethalioid .... b
a. Fructification sporangiate .... d
  b. Capillitial threads unbranched, united into columnar cords and attached both at base and peridium; columella lacking .... 1. *Schenella*
  b. Capillitium branched, dendroid c
c. Columellae obscure or lacking, capillitium not vesicular .. 2. *Amaurochaete*
c. Columellae distinct above, blending beneath; capillitium vesicular .... 3. *Brefeldia*
  d. Columella obscure or lacking .... 4. *Diacheopsis*
  d. Columella present (lacking in *L. insessum*) .... e
e. Hypothallus, stipe and columella calcareous .... 5. *Diachea*
e. Hypothallus, stipe and columella free from lime .... f
  f. Stipe and columella and sometimes capillitium and peridium waxy .... 6. *Elaeomyxa*

f. Stipe and columella neither waxy nor calcareous ....g
g. Capillitium lacking or replaced by a few branches at tip ...7. *Macbrideola*
g. Capillitium well developed ....h
h. Columella percurrent; capillitium arising from a disk at its apex ....8. *Enerthenema*
h. Columella rarely percurrent; capillitium arising from the entire length of the columella or if from the apex, not from a disk i
i. Capillitium brush-like, rigid, ultimate branches bearing at their tips circular disks derived from the peridium .....9. *Clastoderma*
i. Capillitium without conspicuous circular disks at tips of rigid branches ....j
j. Peridium persistent, iridescent ....k
j. Peridium fugacious l
k. Peridium dehiscent into irregular persistent petaloid lobes; capillitium of simple dark threads ....10. *Barbeyella*
k. Peridium as a whole persistent; capillitium freely branching and anastomosing ....11. *Lamproderma*
l. Tips of capillitial branches united to form a more or less complete surface net ....12. *Stemonitis*
l. Tips of capillitial branches not united to form a surface net ....13. *Comatricha*

Stemonitis Gleditsch 1753 is the type of the family Stemonitaceae. In its modern application, it is characterized by distinct or fasciculate, stalked, cylindrical sporangia with a prominent columella usually extending the entire height of the sporangium, or nearly so, and giving rise on all sides to the capillitium which forms a surface net by anastomosis of the many capillitial threads. The peridium of this genus is very evanescent.

The genus *Comatricha* was segregated from *Stemonitis* by Preuss in 1851. The primary character on which the segregation was based is the lack of a surface net in *Comatricha*. The anastomosis of the capillitial filaments in *Comatricha* is general from the columella to the periphery of the sporangium, with the ultimate tips free, not supporting a surface net. In *Stemonitis* the anastomosis of the capillitial filaments ends in the formation of a surface net just beneath the fugacious peridium. Occasionally an imperfectly developed surface net may be observed in species of *Comatricha;* in *Stemonitis,* where a capillitial net is characteristic, it is usually imperfectly developed in *Stemonitis nigrescens* and *S. hyperopta.* The sporangia of *Comatricha* vary in shape from globose to ovoid to cylindrical, the columella extends into the sporangium at least

half-way, bearing branches on every side, and the peridium is more persistent than in *Stemonitis*, sometimes remaining at the base, as in *C. Rispaudii* and *C. cornea* or, in some collections of *C. typhoides*, persistent throughout.

Since there are species of both these genera which show varying degrees of intergradation, the separation may be regarded as useful rather than significant.

The genus *Lamproderma*, which has been critically discussed in the preceding paper, exhibits characters common to both *Stemonitis* and *Comatricha*, but is a little more specialized. In discussing the relationships of *Lamproderma* with the other genera of the family it might not be amiss to regard *Comatricha* as the center for comparison with *Stemonitis* on the one hand, characterized by cylindrical sporangia, fugacious peridium and a long conspicuous columella giving rise on all sides to the capillitium, at the tips of which a conspicuous surface net is formed, and *Lamproderma* on the other, with its globose to ovate sporangia, its rather persistent, iridescent peridium and its branching and anastomosing capillitium arising mainly from the apex of a shorter columella; these two genera in themselves being centers for comparison with other genera of the family (FIG. 1).

Transition from *Comatricha*, with its globose to ovate or cylindrical sporangia, lacking a surface net, and having a partially persistent peridium, to *Lamproderma* with its globose to ovoid sporangia, its much-branched and anastomosing capillitium arising from a typically unbranched columella (*L. arcyrionema* is an exception) can conveniently be traced.

From *Stemonitis, Brefeldia* and *Amaurochaete* are divergent genera and possibly *Schenella*. *Brefeldia* Rost. (Versuch 8. 1873) has an aethalioid type of fructification consisting of confluent sporangia rising from a spongy barren base, columellae blending beneath and capillitial threads which arise from the columellae and unite with adjacent capillitial filaments by means of enlarged, many-chambered vesicles. The connection of the adjacent sporangia of *Stemonitis confluens* by means of the small circular discs on the lateral extensions of the capillitial filaments may be directly compared with the vesicles of *Brefeldia maxima* which unite similar elements.

Amaurochaete Rost. (Versuch 8. 1873) is likewise an aethalioid form with confluent sporangia, a fugacious peridium and an irregular capillitial complex of dark branches which sometimes forms an indistinct surface net, resembling the similar structure present in *Stemonitis.*

Schenella Macbride (Mycologia 3: 39. 1911) is a genus of very doubtful affinities. For convenience it may be included with this group. It has an aethalioid fructification, a pale, fugacious, crust-

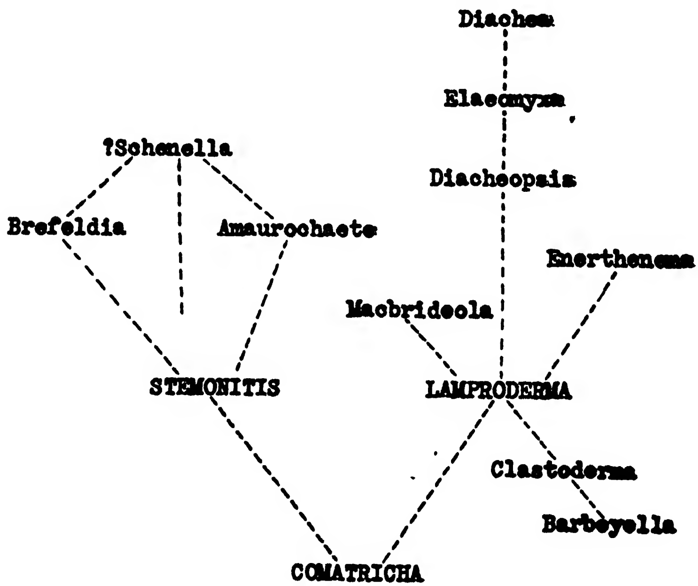


FIG. 1. Suggested relationships of the genera in the Stemonitaceae.

like peridium and abundant, dark brown capillitium, each column of which is made up of a number of twisted threads which form a cord covered in part at least by a sheath.

The following genera may be regarded as exhibiting characteristics which are indicative of relationships to *Lamproderma* with its typically globose, iridescent, stalked, or sessile sporangia with fairly persistent peridium, usually distinct columella from which the much-branched capillitium arises typically at the apex.

Diacheopsis Meylan (Bull. Soc. Vaud. Sci. Nat. **57**: 149. 1930) can best be compared with *Lamproderma insessum,* since both are sessile forms in which the columella is lacking. *Diacheop-*

sis seems to differ from typical Lamprodermas only in the absence of a columella. It is entirely possible that *L. insessum*, the only species of *Lamproderma* lacking a columella, should be transferred to *Diacheopsis*. This, however, would make the presence or absence of a columella the character on which the genera are distinguished. Because the presence or absence of a columella is a relatively unimportant difference on which to distinguish genera, it is suggested that the genus *Lamproderma* might appropriately be emended so as to include a form such as *Diacheopsis metallica*, which has all the other characteristics of *Lamproderma*. However, in the absence of sufficient material of either species for study, this is advanced merely as a suggestion.

Elaeomyxa Hagelstein (Mycologia **34**: 593. 1942) is a difficult genus to place. Hagelstein puts it in a family by itself on the basis of the presence of an oily or waxy substance in the stalk, columella, capillitium or sporangial wall. This segregation seems unwarranted. Its other characters: persistent peridium, capillitium of anastomosing dark threads, columella present or absent and dark spores, are in keeping with the concept of the family Stemonitaceae as here presented. The capillitium of *E. cerifera* is particularly suggestive of the capillitium of *Lamproderma scintillans*. The straight, rigid threads, sparsely branching and anastomosing, with pale tips, are striking in their resemblance to that species.

Diachea Fries (Syst. Orb. Veg. **1**: 143. 1825) is another genus whose relationships have been variously interpreted. In this treatment it is regarded as belonging to the Stemonitaceae, and closely related to *Lamproderma*, because of its iridescent peridium and its capillitium of delicate branching threads both of which are free from lime. The stipe and columella do contain lime but this does not seem sufficient reason for placing it in the calcareous families when lime is lacking in the capillitium and peridium, and when in other characteristics it so closely resembles *Lamproderma*. Therefore in this treatment it is placed as the end group of the family, for it may represent the connecting link between the limeless families and the lime-containing families, which would then, by implication, be derivative.

Enerthenema Bowman (Trans. Linn. Soc. **16**: 152. 1830) is a distinct genus which appears to be close to *Lamproderma*. It has

a well developed columella which extends the entire height of the sporangial cavity, ending in a flattened disc from which the flexuous capillitial filaments descend; the peridium tends to remain as a calyculus around the base of the sporangium.

Clastoderma Blytt (Bot. Zeitung **38**: 343. 1880), a unique genus, is characterized by sparsely branched capillitial threads which bear at their tips fragments of the peridium. It was brought out in the previous paper that *Lamproderma robustum* exhibits this same character to a less marked degree, but the relationship between the two genera is clear.

From *Clastoderma* to *Barbeyella* a transition in peridial characters may be observed. The peridium of *Barbeyella* dehisces in a few large irregular lobes; the dark capillitium radiates from the apex of the columella as in *Lamproderma* and is attached by the tips to the sporangial wall.

Macbrideola Gilbert (Univ. Iowa Stud. Nat. Hist. **16**: 155. 1934) is a genus of uncertain value. It is sporangiate, stipitate, has a fugacious or persistent peridium, a columella which may divide in some sporangia, but whether single or divided extends the entire height of the sporangial cavity and is attached to the peridium at its apex. In this latter respect it approaches *Enerthenema*. The rudimentary capillitium suggests its relationship with *Echinostelium*, which has been removed from the family. However, pending more collections of the two species (one according to Hagelstein) of *Macbrideola* it will be retained in the Stemonitaceae.

DEPARTMENT OF PLANT SCIENCE,
VASSAR COLLEGE,
POUGHKEEPSIE, NEW YORK

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TWO NEW SPECIES OF MONOBLEPHARELLA [1]

Martha E. Springer

(with 51 figures)

Soils collected from localities widely distributed in the Western Hemisphere have yielded a number of isolates of fungi referable to the genus *Monoblepharella*. A study has been made of the development and morphology of the ten isolates producing sex organs, and will be reported in a later paper. Cultures of the original isolates of *Monoblepharella Taylori* Sparrow and *M. mexicana* Shanor were furnished by the authors. It was possible, therefore, to make careful comparisons with the only two members of the genus which have already been described. This study has resulted in the addition to the genus of two new species.

Monoblepharella elongata sp. nov.

Mycelium well developed; hyphae sparingly branched, the branches usually arising at right angles to the main axes, 1.5–4 μ in diameter, the stouter basal portions up to 7 μ; vacuolization reticulate or scalariform; hyphae usually with many irregular swellings. Sporangia narrowly cylindrical or siliquiform, 40–120 μ in length by 5–13 μ in diameter at the widest point, tapering to 2–4 μ at the base, terminal, or after sympodial branching of the hyphae, appearing lateral, usually with one or occasionally several lateral papillate outgrowths near the base. Zoospores emerging through a pore at the apex of the sporangium and through the apices of outgrowths; zoospore with an anterior group of small refractive globules, ovoid or subcylindrical, 6.5–10.5 μ long by 4–6 μ wide, the single posterior flagellum up to 26 μ long. Oogonium at first terminal or, after sympodial branching of the supporting hypha, appearing lateral,

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narrowly obpyriform, 17–35 μ long by 7–12 μ in diameter at the widest point, with rounded apex and a cylindrical base 2–4 μ in diameter, the contents at maturity forming one to three or rarely up to eight eggs containing numerous large refractive globules. Antheridium either terminal on a branch subtending the oogonium and cylindrical, 20–45 μ long by 3–5 μ wide, or hypogynous and geniculate, consisting of a cylindrical section of the suboogonial hypha 2–19 μ long and a beaklike lateral outgrowth 10–35 μ long by 3–5 μ wide. Antherozoids four to seven, emerging through a pore at the apex of the antheridium, strongly amoeboid, ovoid when swimming, 5–6 μ long by 3–4 μ wide, with an anterior group of small refractive globules, posteriorly uniflagellate, the flagellum up to 20 μ in length. Zygote spherical or broadly ovoid, 9–13 μ long by 8–10 μ wide, posteriorly uniflagellate, free swimming or during rest periods strongly amoeboid, containing large refractive globules. Oospore formed free in the water, or occasionally retained within or at the orifice of the oogonium, 9–12 μ in diameter, with a light brown, smooth wall up to 1 μ in thickness, contents bearing globules, upon germination forming a mycelium.

In soil, isolated on hemp seed bait. Soil collected by C. D. LaRue from ditch behind rubber factory, Las Palmas, State of Chiapas, Mexico, February 6, 1941 (type of species). Soil collected by M. E. Springer from marble quarry, Columbia, Tuolumne County, California, March 28, 1942.

Mycelium amplum, hyphis ramosis, tenuibus 1.5–7 μ diametro, reticulate vel scalariforme vacuolatis, plerumque multis irregularibus tumoribus. Sporangia anguste cylindrica vel siliquiformia, 40–120 μ longa, 5–13 μ crassa, basi angustata 2–4 μ crassa, plerumque uno aut rare compluribus papilliformis protrusionibus ad basum; zoosporis ovoideis vel subcylindricis, 6.5–10.5 μ longis, 4–6 μ crassis, uno postico flagello usque ad 26 μ longo. Oogonium hypham terminans, anguste obpyriforme, 17–35 μ longum, 2–4 μ crassum, apice rotundato, basi anguste cylindrico 2–4 μ diametro, ovis 1–3 rare ad 8 cum globulis magnis refractivis. Antheridium aut hypham oogonio subnatam terminans, anguste cylindricum, 20–45 μ longum, 3–5 μ diametro, aut hypogynum, segmenti hyphae suboogonialis 2–19 μ longi et protrusionis rostriformae lateralis 10–35 μ longi, 3–5 μ crassi; antherozoideis 4–7 valde amoeboideis, ovoideis si natantibus, 5–6 μ longis, 3–4 μ crassis, uno postico flagello ad 20 μ longo. Ova inseminata sphaerica vel late ovoidea, 9–13 μ longa, 8–10 μ crassa, uno postico flagello, natantia aut, dum requiescent, valde amoeboidea, globulis magnis refractivis inclusis. Oospora in aqua libere formata sphaerica, 9–12 μ diametro, membrana laevia pallide brunnea, ad 1 μ crassa, globulis inclusis, germinata mycelium formans.

In humo per *Cannabis* semen illecebram culta. Humum legit C. D. LaRue e fossa, Las Palmas, Civitas Chiapas, Mexico, Feb. 6, 1944 (specimen typicum).

Monoblepharella elongata appears to be most closely related to *M. Taylori* Sparrow. The order of development and the arrangement of the organs is the same. The most conspicuous difference between the two species is that which suggested the specific name *elongata* for the new species—a pronounced elongation in *M. elongata* of all of the organs, sporangia, as well as antheridia and oogonia, without a corresponding increase in diameter.

Many of the stages in the morphology and development of *Monoblepharella elongata* are similar to those which have already been described for *Monoblepharis* (Sparrow, **1933, 1943**) and for other species of *Monoblepharella* (Sparrow, **1940**; Shanor, **1942**). The mycelium, like that of other species of *Monoblepharella,* is sufficiently distinctive to identify it as belonging to the genus even in the vegetative condition. It grows very slowly and is so delicate that it is distinguishable even from other members of the *Monoblepharidales,* all of which possess the same type of reticulate or scalariform vacuolization. Globose or irregular swellings (FIG. 9) occur in great abundance on the hyphae of *M. elongata.* Such nodules are found to some extent on the hyphae of all other species (Sparrow, **1940**; Shanor, **1942**), but not in such large numbers. They are considered to be normal structures, probably acting as reservoirs of protoplasm for subsequent vegetative growth.

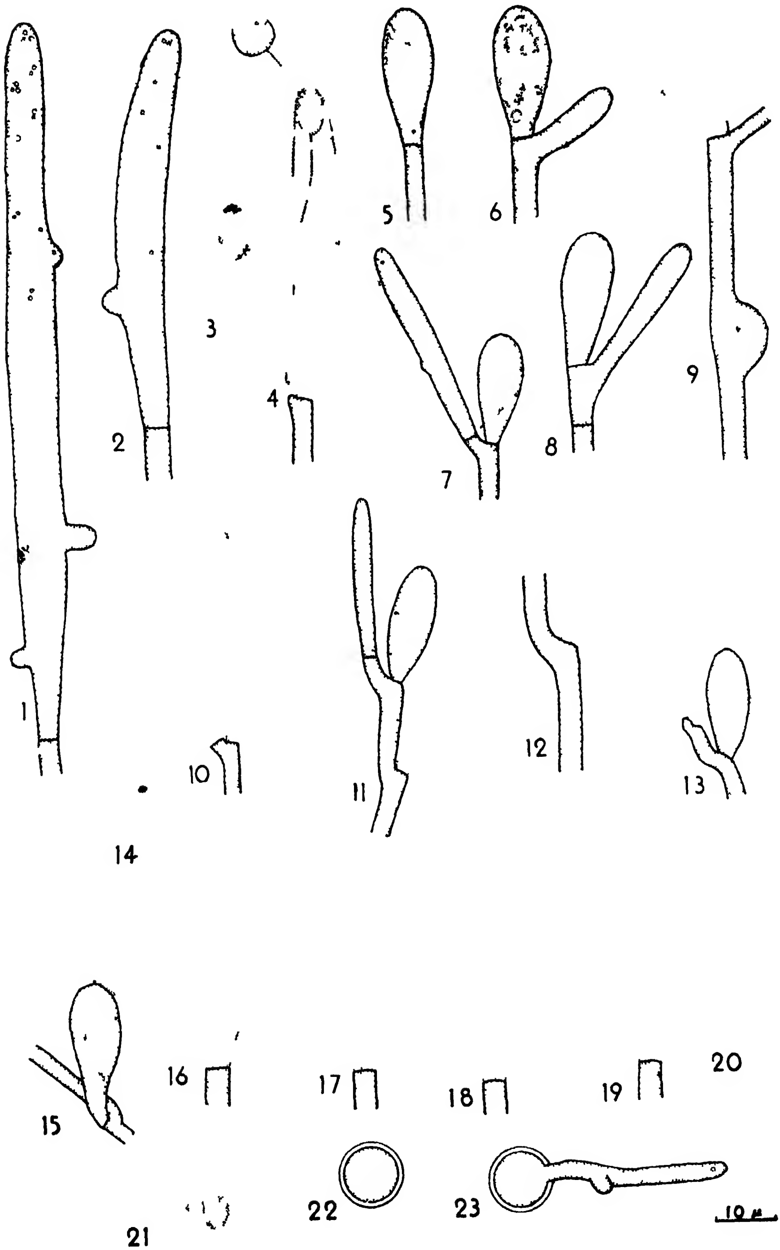
In undisturbed cultures only a few reproductive organs will develop at any one time. Although both nonsexual and sexual organs are occasionally found simultaneously, more typically either the one or the other is formed under given conditions. It has been found that production of sporangia is stimulated by the sudden starving of the mycelium by placing it in fresh water at a temperature preferably between 21 and 31° C. Sex organs are formed in abundance only when the mycelium is left undisturbed for several days at constant temperatures ranging from 26–32° C., with the optimum in this species from 26–27° C.

By reason of their refractive appearance and large size as compared with the delicate mycelium, the sporangia of *Monoblepharella elongata* are very conspicuous. Although there is much overlapping in the measurements of the sporangia of this and of other species, the average length in *M. elongata,* 75 μ, is much greater while the average width, 8.6 μ, is somewhat less. The mean ratio

of length to diameter is more than one and one-half times that of *M. Taylori.* The presence of lateral papilla-like projections has been mentioned for *M. Taylori* and *M. mexicana,* but in both of these species they occur only rarely. The sporangia of *M. elongata* (FIGS. 1, 2, 4) typically bear one or more of these lateral projections which are used as additional exit tubes, although the majority of the zoospores escape through the apex. The zoospores in the manner of their escape and appearance (FIG. 3) are indistinguishable from those described for other species.

Both oogonia and antheridia are at once distinguished from those of congeneric forms by their long narrow shape and the frequency with which more than one egg is formed in the oogonium. The method of development and the resulting arrangement of sex organs are like those described in *Monoblepharella Taylori* (Sparrow, **1940**). The oogonial rudiment develops terminally on a hypha (FIG. 5). Small oil droplets coalesce to form the large globules (FIG. 6) characteristic of the mature egg. Although at first they fill the oogonium, later the globules are found only in the central portion, leaving an area of clear protoplasm at the tip and at the base. At maturity the egg rounds up and withdraws from the base of the oogonium. If more than one egg is to be formed in the oogonium, this is indicated by a characteristic grouping of the oil globules before the actual delimitation is noticeable. In about one-half of the oogonia more than one egg is produced. The number is usually from one to three, although eight were observed in a single oogonium (FIG. 12). This is in striking contrast to the other species where it is only rarely that an oogonium contains more than one egg.

Antheridial growth is initiated by the development of a short lateral branch arising immediately beneath the oogonial cross wall (FIG. 6). The antheridium may be terminal (FIGS. 7, 11) or hypogynous (FIGS. 8–11), with both types sometimes found even on the same branch (FIG. 11). The antheridia average about eight times as long as wide, while in *M. Taylori* this ratio is only about three to one. The emergence of the antherozoids (FIG. 13) is similar to that of the zoospores. While emerging the antherozoid is round or irregular at first, but when swimming it resembles a small zoospore (FIG. 14). When it is moving about on the surface



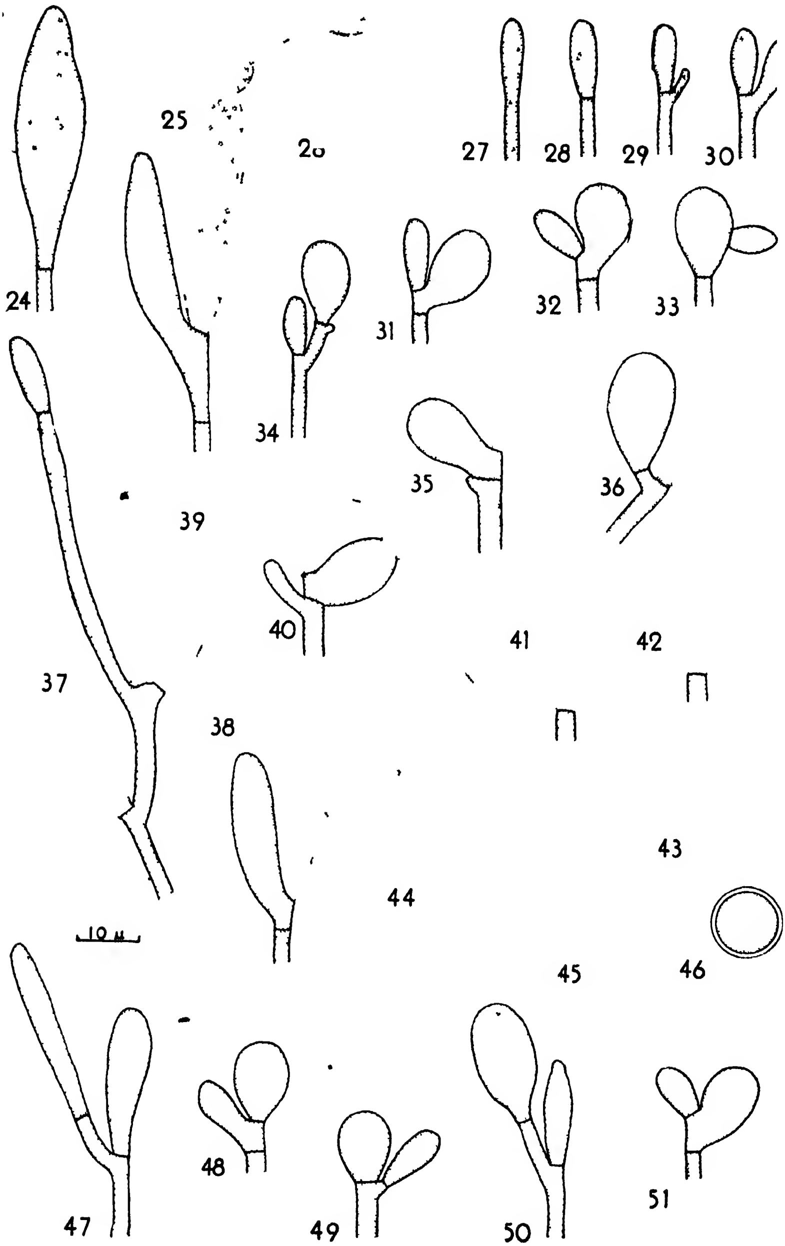
FIGS 1–23 *Monoblepharella elongata*

of an oogonium (FIG. 15), it is strongly amoeboid, its flagellum remaining passive, or waving weakly about in the medium. Fertilization and the emergence of the zygote (FIGS. 16–19) occur precisely as in *M. Taylori*. Indeed, save for the difference in the shape of the sex organs, the figures of this process as occurring in *M. Taylori* (Sparrow, **1940**) could be used for any of the species studied. The zygote (FIG. 20) too is characteristic of the genus. As it swims with a rolling, halting and rocking movement, it progresses so slowly that it is frequently possible to see the moving posterior flagellum. The flagellum may be visible throughout the entire period of fertilization, emergence, and the early swimming stages, thus giving definite evidence that it is, as Sparrow contended, the flagellum of the antherozoid which is used for the propulsion of the zygote. As the zygote rolls and turns the globules are easily distinguishable and seem to form a compact peripheral layer lining all except the broadly conical anterior end. Motility may continue for a period of at least half an hour, during which time it frequently stops to rest or to undergo strong amoeboid crawling (FIG. 21). Finally it encysts and becomes surrounded by a smooth thickened wall (FIG. 22).

Germination of the oospores may be obtained by adding fresh water and bait to an old culture or to the dried spores. It is not known how long the spores will remain viable, but growth of this species was obtained from dried soil from the original sample three years after collection. Germination is by a hypha which protrudes through a pore formed in the wall of the oospore (FIG. 23). This primary vegetative element almost immediately assumes the vacuolate condition typical of the mature mycelium.

Monoblepharella Laruei sp. nov.

Mycelium well developed; hyphae sparingly branched, the branches usually arising at right angles to the main axes, delicate, 1.5–4 μ in diameter, the stouter basal portions up to 7 μ; vacuolization reticulate or scalariform; hyphae with occasional swellings. Sporangia cylindrical or siliquiform, 28–82 μ long by 7–15 μ in diameter at the widest point, occurring at the tips of hyphae, or several often developed in basipetal succession, later sporangia sometimes geniculate. Zoospores emerging through a pore at the apex of the sporangium, ovoid or somewhat cylindrical, 7–9 μ long by



FIGS. 24–26, *Monoblepharella Laruei*, 47, *M. elongata*; 48 and 49, *M. Taylori*; 50, *M. mexicana*; 51, *M. Laruei.*

5–5.5 μ in diameter, with an anterior group of small refractive globules, posteriorly uniflagellate, the flagellum up to 27 μ in length. Oogonium terminal on a branch subtending the anteridium, or formed by a swelling of the hypha below the antheridium, after sympodial branching of the hypha appearing lateral, obpyriform, 11–20 μ long by 7–12 μ in diameter at the widest point, with rounded apex, and, if terminal, with narrowly cylindrical base tapering to 2–4 μ, the contents at maturity forming one or rarely up to three eggs bearing numerous large refractive globules. Antheridium always formed terminally on the hypha, later often epigynous, 8–19 μ long by 4–7 μ in diameter at the widest point. Antherozoids two to five, emerging through a pore at the apex of the antheridium, strongly amoeboid, ovoid when swimming, 4–5 μ long by 3–3.5 μ wide, with an anterior group of small refractive globules, posteriorly uniflagellate, the flagellum up to 19 μ in length. Zygote spherical or broadly ovoid, 10–13 μ long by 8–10 μ wide, posteriorly uniflagellate, free swimming, amoeboid during rest periods, the contents bearing numerous large refractive globules. Oospore formed free in the water, spherical, 9–13 μ in diameter, with a light brown, smooth wall up to 1 μ in thickness, contents bearing globules, germination not observed.

In soil, isolated on hemp seed bait. Soil collected by C. C. LaRue: stream bank mud, Cooper Landing, near Bluefields, Nicaragua, December 28, 1940 (type).

Mycelium amplum, hyphis ramosis, tenuibus 1.5–7 μ diametro, reticulate vel scalariforme vacuolatis, spatio interiecto tumoribus. Sporangia cylindrica vel siliquiformia 28–82 μ longa, 7–15 μ crassa, terminalia vel saepe plura basipetaliter producta; zoosporis ovoideis vel cylindricis 7–9 μ longis, 5–5.5 μ crassis, uno postico flagello usque ad 27 μ longo. Oogonium hypham antheridio subtenentem terminans aut e hypha sub antheridio tumescente formatum obpyriforme, apice rotundata 11–20 μ longum, 7–12 μ crassum, et si terminale basi anguste cylindrico 2–4 μ diametro; ovis singulis rare ad 3 cum globulis magnis refractivis. Antheridium semper hypham terminans, postea aliquando epigynum 8–19 μ longum, 4–7 μ crassum; antherozoideis 2–5 valde amoeboideis, ovoideis si natantibus, 4–5 μ longis, 3–3.5 μ crassis, uno postico flagello ad 19 μ longo. Ova inseminata sphaerica vel late ovoidea 10–13 μ longa, 8–10 μ crassa, natantia, dum requiescent amoeboidea, magnis refractivis globulis inclusis. Oospora in aqua libere formata, sphaerica, 9–13 μ diametro, membrana pallide brunnea laevia ad 1 μ crassa, magnis refractivis globulis inclusis, germinatione ignota.

In humo per Cannabis semen illecebram culta. Humum legit C. D. LaRue e luto in rivi ripa, Cooper Landing, ad Bluefields, Nicaragua, December 28, 1940 (specimen typicum).

This fungus is dedicated to Dr. C. D. LaRue of the University of Michigan, who furnished a large number of the soil samples from which were obtained isolates of *Monoblepharella,* including the type isolates of *M. Laruei and M. elongata.*

The mycelium of *Monoblepharella Laruei* is typical for the genus. Some nodules are present although not in such great quantity as on hyphae of *M. elongata.* Sporangia are produced in great abundance when the mycelium is put into fresh water between temperatures of 21–31° C. They develop terminally on the hypha (FIG. 24) and in shape and size closely resemble those of *M. Taylori.* Secondary sporangia (FIGS. 25, 38) however, are formed in basipetal succession rather than in the sympodial manner characteristic of the other species. This type of sporangial formation has been found to occur in a few instances but not typically in cultures of *M. mexicana.* The swelling below the cross wall of the primary sporangium develops directly into a geniculate sporangium, which is then delimited basically from its attendant hypha by a cross wall. Sporangia may continue to form in this manner. Usually as each sporangium develops it comes to lie with its long axis in line with that of the hypha. The first formed sporangium now appears to be a lateral outgrowth from the mature secondary organ. Sporangial discharge and the zoospores (FIG. 26) are like those of other species.

Development of the sex organs proceeds in just the reverse order from that of *Monoblepharella elongata* and *M. Taylori,* starting with the formation of the antheridium, as in *M. mexicana.* The antheridium is formed by the swelling of a hyphal tip (FIG. 27) and the laying down of a cross wall (FIG. 28). The mature antheridium has the smallest average length (11 μ) of any of the isolates studied. The lateral outgrowth (FIG. 29) which soon forms beneath the antheridial cross wall may develop into a short branch, and produce a terminal oogonium (FIG. 34), or it may expand to form a subantheridial oogonium (FIGS. 30, 31). This method of oogonial development corresponds closely to that of the hypogynous antheridia of *M. Taylori* and *M. elongata.* When the oogonium is first cut off, the antheridium, although now epigynous, lies in a direct line with the long axis of the hypha. Frequently, however, the oogonium rather than the antheridium comes

to lie in this position, and the antheridium then appears lateral (FIGS. 32, 33). Occasionally a second female gametangium may be cut off immediately below the first (FIG. 35). By later sympodial branching of the hypha, the sex organs may assume a lateral position (FIG. 37).

The sequence of stages in the formation of the egg, involving the coalescence of oil droplets to form large globules, progresses as in other species. Rarely more than one egg may be formed in an oogonium (FIG. 36). Fully mature oogonia are obpyriform or geniculate, depending upon whether they are terminal or intercalary.

Sex organs have been developed abundantly in cultures kept at constant temperatures of between 26 and 32° C. If the culture is disturbed or removed from the oven, sporangial development will commence. Occasionally in such conditions sporangia will be formed basipetally beneath sex organs (FIG. 38).

Because of the small size of the antheridium, frequently there are only two antherozoids produced in each. The largest number observed in a single antheridium was five. The emergence of the antherozoids (FIGS. 36, 40, 41), their appearance when swimming (FIG. 39), fertilization (FIG. 40) and the emergence and the swarming of the zygote (FIGS. 41–45) are like these stages in other members of the genus. Large numbers of resting spores may be found in an old culture, but their germination has not as yet been observed.

Resemblances have been pointed out between *Monoblepharella Laruei* and *M. mexicana* and also between *M. elongata* and *M. Taylori*. Distinctive characteristics of the four species are emphasized by a comparison of drawings of typical pairs of sex organs. The organs of *Monoblepharella elongata* (FIG. 47) are much longer and comparatively narrower than the more rounded organs of *M. Taylori* (FIGS. 48, 49). In both of these fungi the oogonium is produced before its attendant antheridium, and the antheridium may be either terminal or hypogynous. In *Monoblepharella mexicana* (FIG. 50) and *M. Laruei* (FIG. 51) the oogonium develops after its attendant antheridium. In *M. mexicana* both organs are produced terminally on the hyphae, while in *M. Laruei* the oogonium is frequently epigynous.

SUMMARY

Two new species of *Monoblepharella* have been recovered from soil samples, *Monoblepharella elongata* from Mexico and California and *Monoblepharella Laruei* from Nicaragua. *Monoblepharella elongata* in the development and arrangement of its organs resembles *M. Taylori* Sparrow. It differs from Sparrow's species in the large number of nodules on the mycelium, the presence typically of lateral projections on the zoosporangia, the frequent formation of several eggs in the oogonia, and, most conspicuously, in the greater length and slenderness of its reproductive organs. *Monoblepharella Laruei* is the only known species of *Monoblepharella* in which epigynous antheridia may occur. This, the small size of the antheridia, and the formation of secondary zoosporangia almost exclusively in basipetal fashion are the chief characteristics which separate it from the closely related *M. mexicana* Shanor.

ACKNOWLEDGMENTS

The writer wishes to express her appreciation to Dr. C. D. LaRue for the use of the soils from which the new species were isolated, to Dr. Leland Shanor for the culture of *Monoblepharella mexicana*, and to Dr. F. K. Sparrow for the culture of *M. Taylori*. She is especially indebted to Dr. Sparrow for his helpful suggestions during the investigation and the preparation of this paper.

DEPARTMENT OF BOTANY AND BACTERIOLOGY,
INDIANA UNIVERSITY,
BLOOMINGTON, INDIANA

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EXPLANATION OF FIGURES

All drawings were made with the aid of a camera lucida and are approximately × 758 as here reproduced.

FIGS. 1–23, *Monoblepharella elongata.* 1, large zoosporangium with three lateral projections; 2, zoosporangium of average size; 3, zoospore; 4, zoosporangium showing late stage in emergence of zoospores; 5, young oogonium; 6, older oogonium and antheridial rudiment; 7, sex organs, with antheridium terminal; 8, sex organs, with antheridium hypogynous; 9, empty sex organs on a portion of mycelium bearing a nodule; 10, branch with two closely adjacent pairs of sex organs; antheridia hypogynous in both; 11, two pairs of sex organs, showing both terminal and hypogynous antheridia on the same branch; 12, large oogonium with eight eggs; 13, stage in emergence of antherozoids; 14, antherozoid; 15, antherozoid on tip of oogonium: 16–19, fertilization and stages in the emergence of the zygote; 20, typical motile zygote; 21, zygote with shape assumed during periods of amoeboid movement; 22, oospore; 23, germination of oospore.

FIGS. 24–46, *Monoblepharella Laruei.* 24, typical sporangium; 25, stage in discharge of zoospores from a terminal sporangium which is subtended by a basipetally formed secondary sporangium; 26, zoospore; 27–33, stages in development of sex organs, showing terminal development of antheridium, and subsequent development of oogonium so that the antheridium appears to be epigynous; 34, hyphal tip on which both the antheridium and the oogonium were formed terminally; 35, antheridium subtended by two oogonia produced in basipetal succession; 36, large oogonium with the two eggs; antheridium from which antherozoids are emerging; 37, portion of hypha showing sequence of sex organs; 38, hyphal tip showing basipetal development of four sporangia beneath an oogonium and epigynous antheridium; 39, antherozoid; 40, antherozoid about ready to fertilize egg; 41, 42, stages in emergence of zygotes; 43, typical motile zygote; 44, 45, shapes assumed by zygote during periods of amoeboid movement; 46, oospore.

FIGS. 47–51, typical sex organs of four species of *Monoblepharella.* 47, *M. elongata;* 48, 49, *M. Taylori;* 50, *M. mexicana;* 51, *M. Laruei.*

A CYTOLOGIC STUDY OF SEVERAL SMUT FUNGI

ELISA HIRSCHHORN [1]

(WITH 3 FIGURES)

In spite of the fact that the Ustilaginales, from the biologic and economic point of view, are one of the most important groups of parasitic fungi in the world, not much has been done to explain the biological phenomena associated with the behavior of their nuclei. Most of the work has been done in taxonomy and in the life history and physiology. Genetic knowledge of smuts, especially those which parasitize cereals, such as *U. Zeae, U. levis, U. Hordei,* etc., shows that the chlamydospores possess diploid nuclei, which migrate to the young promycelia when the chlamydospores germinate, and that the first and second nuclear divisions take place in the promycelium, resulting in the formation of four cells, each containing one haploid nucleus (4, 5, 6, 13, 14, 17, 18). According to Hanna (8), Christensen (2) and others (11, 16), reduction may take place in the first, second, or later nuclear divisions. These genetic studies have been confirmed by cytologic investigations. In fact, Wang, D. T. (18) showed cytologically, in *U. Avenae, U. levis, U. Hordei, U. nuda, U. violacea, U. longissima,* etc., that reduction may take place in the first or second nuclear division. These species have two pairs of chromosomes, the first nuclear division being reductional and the second equational. The first division may take place inside the spore at the moment when germination begins, the reduced nuclei migrating to the young promycelium,

[1] Assistant in Plant Pathology, The State College of Washington, Pullman, Washington.

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or in other cases all division may take place in the promycelium. Recently Wang, C. S. (17) showed that *U. Crameri* also has two pairs of chromosomes and that meiotic division may take place in the first, second, or third nuclear division. These caryologic studies are the physical basis which explains genetic segregation observed in the species of *Ustilago* mentioned above, and the formation of many physiologic races, but they do not explain why some species, for example *U. Zeae,* are made up of an indefinite number of physiologic forms, more than is possible to expect by segregation and recombination. Christensen (2) has studied a large number of different sexual types of segregation in *U. Zeae.* He believed, like Stakman (16), that existence of so many different sexual groups and so many different physiologic forms in this species may be due, in part, to late reductional characters. Nuclear behavior in very few other species has been studied. In *U. longissima, U. Zeae,* and *Tilletia Tritici* the haploid number of chromosomes is also two (18). It is evident that more study of the nuclear process in smut fungi is needed.

As a part of a more extensive and detailed cytologic work, some preliminary observations on nuclear behavior of *U. Williamsii, U. Spegazzinii* var. *agrestis, U. halophila* and *Sorosporium consanguineum* are presented here. Different stages in nuclear division in the promycelium, sporidial and hyphal formations, and some abnormalities in these will be described. The first three species listed are stem smuts and the fourth a flower smut. *U. Spegazzinii* var. *agrestis* and *U. Williamsii* have a similar peculiarity of morphology: both have prolongations of the epispore, although these prolongations are different in nature. In the second species they are hyaline, while in the first they are the same as the epispore. Probably this may involve some relationship. In some years *U. Spegazzinii* is of economic importance, being endemic in the northwestern part of the United States and in La Plata, Argentina.

MATERIAL AND METHODS

The material used in the present study was kindly supplied by Dr. G. W. Fischer. It was collected in Montana, Washington, and Idaho and consisted of *Ustilago Williamsii* on *Stipa Richardsoni,* from Butte, Mont., 1941; *U. Spegazzinii* var. *agrestis,* on *Agro-*

pyron Smithii, Pullman, Wash., 1943; *U. halophila,* on *Distichlis stricta,* Blue Lake, Idaho, 1940: *Sorosporium consanguineum,* on *Aristida longis,* Whitebird, Idaho, 1941.

The spores were germinated in an aqueous solution containing 2 per cent dextrose, 1 per cent maltose, and 0.5 per cent peptone extract. The slides were covered with a very thin film of egg albumin. After spreading a drop of nutrient solution on the slide, the spores were dusted on by means of a thin brush. The slides were then placed in a moist petri dish, inside an incubator, at 22–25° C. When the desired stages were reached, the spores on the slides were killed and fixed with Fleming's weak solution by putting several drops of the solution on the slide and leaving it 20–25 minutes, after which period the liquid was removed with filter paper. When dry, the material was bleached by placing the slides in a 10 per cent solution of hydrogen peroxide for 20 minutes, after which they were washed in distilled water 3–5 minutes. The slides were then placed in 4 per cent iron alum 4–6 hours and washed in distilled water 2–3 minutes. Staining was done in an aqueous 0.5 per cent solution of haematoxylin for 18–24 hours, following which the slides were washed in running water 10 minutes and then 10 minutes in distilled water, changing two or three times, as suggested by Rawlins (15). Dehydration was begun with 15 per cent alcohol, allowing 2 minutes in each grade. After 95 per cent alcohol the material was destained in acid alcohol for about 10 seconds, and then placed again in 95 per cent and finally in 100 per cent alcohol. Clearing was done in clove oil which was washed out with two changes of xylol. The stained preparations were mounted in balsam. Other fixatives used included Craf's, Bouin's and a solution made up of 3 parts of absolute alcohol and one part of glacial acetic acid, and other stains used included Crystal Violet and Triple Stain, but Fleming's weak solution and haematoxylin gave the best results.

RESULTS

USTILAGO WILLIAMSII (Grif.) Lavr.

Spores dark olivaceous-brown, globose to subglobose, 7–10 μ in diameter; epispore smooth and deeply cracked, bearing two bipolar

appendages. Germination begins after 12 hours storage under favorable conditions. Behind the appendages a tube emerges which in a few hours reaches complete development, forming a 4–8 celled promycelium, which soon begins to form branches, and in many cases these branches developed secondary branches. In the culture medium used in this study such sporidia did not appear (10).

Nuclei behavior. The nuclear behavior as observed in various stages of development in this species is illustrated in figure 1. The mature chlamydospore contains one nucleus which apparently is diploid (FIG. 1: 1). This is similar to the nuclear conditions observed in other smut fungi (4, 13, 14, 17, 18). Apparently the first nuclear division sometimes occurs in the spore but in most cases in the very young promycelium. This nucleus migrates to the promycelium as soon as a short tube appears, usually without previous division (FIG. 1: 2, 4). Division stages inside the spores were not observed. The only suggestion that such division occurs is the presence of nuclei inside the spore after a long promycelium has developed and the occurrence of bipolar germination (FIGS. 1: 17, 22). When bipolar germination does occur, nuclear division must occur inside the spore and when the promycelium emerges, one nucleus migrates into the larger promycelium while the other seems to remain for a longer time, apparently undergoing a new division inside the spore (FIG. 1: 17, 22). It was not possible to observe many prophase stages. In the few cases observed, the nuclear structure was as illustrated in figure 1: 2 and 3, which appears to be more a resting stage. There is a thin reticulum, a nucleolus and a very thin nuclear membrane. Soon after the nucleus reaches the young promycelium, some times at the base and sometimes at the apex, it is possible to observe four deeply stained bodies which have the appearance of chromosomes in the metaphase (FIG. 1: 4). They soon separate and only two chromosomes are observable in each group in the anaphase (FIG. 1: 5). The second division follows without a resting stage, or at least a resting stage was not observed. Figure 1: 6 and 7 show the second anaphasic stage of such a division with two chromosomes in each one. According to the preceding consideration, the first nuclear division was reductional and the second equational, and the diploid number

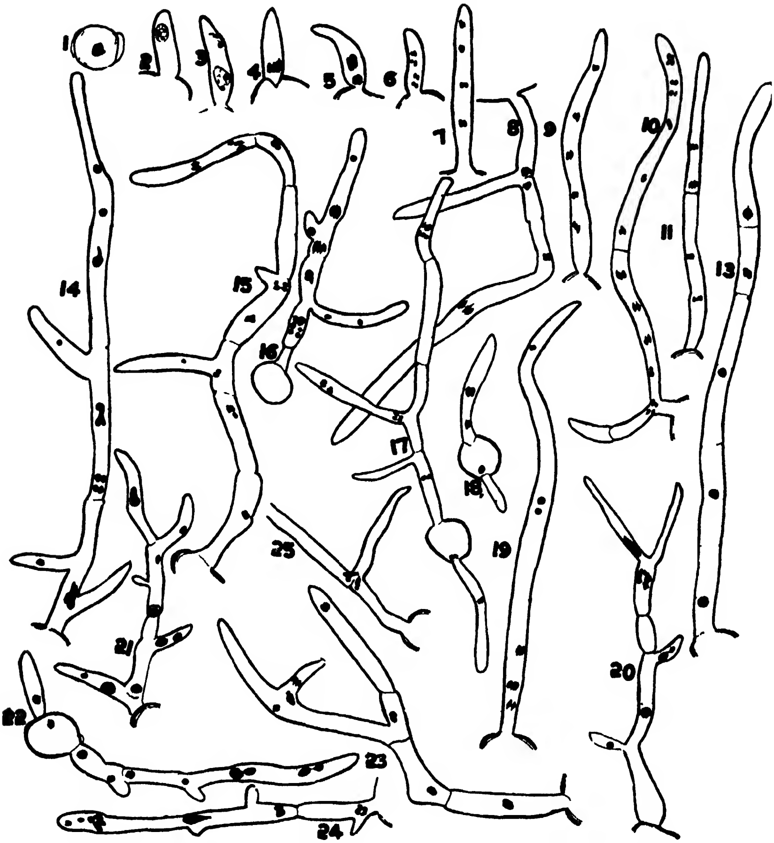

FIG. 1, *U. Williamsii.* 1, mature chlamydospore with a diploid nucleus; 2 and 3, young promycelia with one and two nuclei, respectively, in resting stage or very young prophase stage; 4, metaphase I, with four chromosomes; 5, anaphase I, 6, early anaphase II showing reduced number of chromosomes; 7, late anaphase II; 8 and 25, promycelia in which it is possible to observe a branch borne between adjacent cells, the breaking of the cross wall, the nuclear migration and the beginning of the dicaryophase; 9, late anaphase II or early telophase II; 10, promycelium with several nuclei, some in anaphase stage, just before branching and with the first cross wall formed; 11, four nuclei with the unreduced number of four chromosomes in each; 13, promycelium with a resting nucleus in each cell; 14 and 15, promycelia and branches with nuclei in different division stages (in this illustration cells without nuclei are shown); 16 and 17, promycelia with nuclei in third and fourth division stages, in which it seems that reduction did not take place; 17, bipolar germination in which more than two chromosomes appear in each nucleus; 18, the same as in figure 17, but with reduced nuclei; it is possible to observe that when nuclear division takes place inside the spore, one remains inside longer than the other; 16 and 20–24, dark bodies in variable number which seem to be chromatic or nuclear substance.

of chromosomes in this species is four. The promycelium elongates and soon a third equational division occurs and the four resulting nuclei enter telephase or undergo a new equational division (FIG. 1: 9, 10).

Figure 1: 10 shows a large promycelium with many nuclei, several of them in anaphase, in which it is possible to observe thread connections. Most of these seem to represent the late anaphase or early telephase. At the base there are short branches in which it is possible to observe a division at anaphase and it seems probable that one nucleus will migrate to the branch. In the same figure the first wall is clearly presented, dividing the promycelium into two cells. As soon as these nuclear divisions are finished, cell division is completed. In figure 1: 13 is shown a 5 celled promycelium with one nucleus in early anaphase and the others apparently in resting stages, each having a very thin membrane and deep stained nucleolus. In the resting haploid nuclei, a nuclear reticulum was not observed, but always a nucleolus located in a clear zone surrounded by a thin membrane. This corroborates Wang's (18) observations in *U. Avenae, U. levis,* etc., who said that "the haploid nuclei take the stain always in the same form: "the nucleolus is strongly stained and located in the nuclear cavity which is hyaline." If this is true, it is possible to take this characteristic to distinguish diploid from haploid nuclei.

According to the foregoing considerations, and as shown in figure 1: 4 to 7 and 9, and 10, the first nuclear division is reductional and the second equational. But, on the other hand, there is evidence that reduction division may take place in the second, third, or later nuclear divisions. Figure 1: 11 shows a promycelium with four nuclei in metaphase of the third division in which it is easy to count four chromatic bodies. Figure 1: 16 and 17 represent more advanced stages, and it seems that here reduction division did not take place, because there are infection hyphae. Apparently the number of chromosomes would have been reduced in the hyphae (FIG. 17). Sometimes secondary hyphae bear unreduced nuclei (FIG. 1: 23). Consequently no reduction took place in the first, second or third nuclear division. In contrast to this, in other cases, reduction division was not simultaneous for all the chromosomes

in the same stage nor at the same time. In fact, figure 1: 8, 15, and 19, show nuclei with two and three and four chromosomes.

There were observed in the promycelia and the infection hyphae of individual germinating spores many deeply stained bodies, variable in size and irregularly distributed, either in groups or singly. These bodies take the stain in the same manner as the nuclei (FIG. 1: 16, 20, 21, 24). In many cases these bodies appear along with the typical nuclei, in others they occur instead of the typical nuclei. Wang (**18**), in her study on *U. Avenae, U. Hordei,* etc., describes the behavior of the cytomes and vacuomes. These bodies are of vacular nature and stain deeply with haematoxylin. The illustrations of such bodies shown in Wang's paper suggest, in some respects, the kind of bodies observed in *U. Williamsii.*

Hyphae formation. Sometimes in the early stages of the development of the promycelium, in which reductional or equational nuclear division takes place, or in later stages, small branches begin to emerge from the promycelial cells and one nucleus migrates into each branch. Occasionally nuclear migration occurs when the branch is longer. Figure 1: 14 and 15 show young branches produced by means of the elongation of a promycelial cell containing one nucleus. It seems that these nuclei are produced just before branches begin, or very near to that time (FIG. 1: 20, 23). There are other types of hyphal formation, one of which is by means of fusion between adjacent cells. When this occurs, the wall which divided the cells begins to disappear and there emerges a short tube which contains the protoplasm of both cells. When this tube elongates, it seems that nuclear movement in the direction of the new hypha begins (FIG. 1: 8, 25). This marks the beginning of the dicaryophase (FIG. 1: 17). When reduction division takes place in the primary hyphae (FIG. 1: 12), the nuclei of the secondary hyphae are apparently haploid for all chromosomes and the dicaryophase begins in the secondary hyphae. The nuclear conditions were observed in only a few secondary hyphae, but it seems that there are secondary hyphae with and without the chromosomes reduced. Figure 1: 23 shows a secondary hypha with unreduced nucleus.

Therefore, it seems that there are three different kinds of hyphae: one that originates in one cell and has one or two reduced nuclei;

one that originates from two adjacent cells and has two conjugated nuclei; and another which originates from a single cell and has nuclei which are not reduced for all chromosomes.

USTILAGO SPEGAZZINII var. AGRESTIS Fisch. & Hirsch.

Ustilago Spegazzinii var. *agrestis* is characterized by dark-brown spores; smooth or very finely papillose epispore with bipolar crest, which varies from the entire apical thickenings to conspicuous, deeply dentate crest, hyaline, subhyaline to concolorous with the spore. Spores germinate after 40 hours at 25° C. A single germ tube emerges, elongates, and soon becomes differentiated more or less into a 3–4 celled promycelium, developing long branches. Occasionally a sporidium is formed at the tip of one or more of these branches. Sporidia were observed on plain or dextrose agar (7), but never in the nutrient solution used in the present studies. They branch and rebranch to initiate a mycelium.

Nuclear behavior. Mature chlamydospores contain one diploid nucleus each. At the beginning of germination the nucleus migrates toward the young tube when it is very short (FIG. 2 B: 1, 2). Nuclear division was observed inside the spore in only a very few cases, and it was impossible to determine the nuclear conditions. Figure 2 B: 1 and 3 show young prômycelia with nuclei in the early metaphase with, apparently, four chromosomes in each one. Soon the promycelia elongate and it is possible to observe different anaphase stages in progress (FIG. 2 B: 4, 6), each having 2 chromosomes in each group. It seems that second nuclear division follows immediately and sometimes a third division. At this moment a cell wall appears forming two promycelial cells and as soon as the nuclei enter telaphase, the formation of the other walls begins, dividing the promycelium into 3–5 cells (FIG. 2 B: 7–11). In the nuclear behavior just described the first division is reductional and the second equational. The resting stages apparently are not produced, or, if they are produced, they are so short that they are not readily observed. Reduction does not always take place in the first division, as shown by the fact that 2 groups of 3 chromosomes each have been seen in the second metaphase stage (FIG. 2 B: 12). The nuclei divide a third time, again forming two nuclei just before branching of the promycelium begins.

Two kinds of hyphae were produced. Both were binucleate but one originated from fused adjacent cells and the other from individual cells. In the first case the nuclei do not always migrate simultaneously, but one may remain longer than the other in the promycelium cell (FIG. 2 B: 11).

In the older promycelium (FIG. 2 B: 13) resting nuclear stages were observed. The deeply stained nucleolus was located in a hyaline cavity surrounded by a very thin membrane, such as in *U. Williamsii* and in the species studied by Wang (**18**).

USTILAGO HALOPHILA Speg.

Chlamydospores yellow or yellow-brown, globose, sub-globose to slightly irregular, 5–7 μ diam. or 4–6 × 7–8 μ diam.; epispore smooth. The spores germinate after 8–12 hours at about 25° C. The promycelium elongates rather rapidly and soon becomes septate. Sometimes fusions occur between the cells of the promycelium which then give rise to infection hyphae. On plain agar, or in dextrose malt agar, sporidia often arise from the promycelial cells, or from the branches of the promycelium (**10**). In the cultures used in these studies sporidia were observed infrequently.

Nuclear behavior. The mature chlamydospores are uninucleate and the single nuclei are diploid as in other species. The first nuclear division may take place in the spore or in the promycelium. Inside the spore either one or two nuclei were observed. Presence of two nuclei indicates a preliminary division within the spore. Neither stages of division nor chromosomic behavior inside the spores was observed. Figure 2 A: 1 and 3 show very young promycelial tubes in which the nuclei migrated without a preceding division inside the spore, and in contrast to this, figure 2 A: 2 shows a spore in which the nucleus divided inside the spore and one nucleus migrated to the young promycelium while the other remained inside near the promycelium. The nucleus divides and one daughter nucleus migrates to the apex, as shown in figure 2 A: 4; the promycelium elongates and sometimes resting nuclear stages are observed (FIG. 2 A: 5). The promycelium elongates and there follows a second division after which a wall appears between each pair of nuclei. These walls divide the promycelium into 3 or 4

cells (FIG. 2 A: 7, 14, and 17). It was not possible to determine when reductional or equational nuclear divisions occur. In figure 2 A: 4, which represents a late telephase stage, it seems that each group contains two chromosomes, but in contrast to this, figure 2 A: 17 shows a very long promycelium containing nuclei with what appears to be more than two chromosomes. It seems more logical to consider that the last case (FIG. 17) represents an unreduced nucleus, and that before sporidial formation the nucleus undergoes another division, which would seem to be reductional. Although the promycelial cells usually fused and formed hyphae, some promycelia were observed to produce sporidia without fused cells.

Hyphae formation. There are two kinds of hyphal formation: One kind originates from adjacent fused cells and the other from fused alternate cells, the fusion in the latter case being accomplished by means of tubes. In the first case, when branching starts, a swollen point "knee joint" begins to form. At this point it is possible to observe the cell walls rupture and push out to the new formation which is followed by nuclear migration (FIG. 2 A: 8, 9, 10, 19). Sometimes the nuclei migrate simultaneously and at other times separately (FIG. 2 A: 10, 15). The knee joint seems to originate by means of elongation of the promycelial membrane, which results in the migration of the protoplasm of the involucrate cells, followed by the rupture and partial projection of the wall of the adjacent cell. Afterwards this membrane seems to split (FIG. 2 A: 8, 10,

FIG. 2 A, *U. halophila.* Figs. 1 and 3, germinating chlamydospores, each with a diploid nucleus in the young promycelium; 2, one nucleus in the promycelium and one in the spore, indicating that nuclear division took place in the spore; 4, first late anaphase or early telphase stage with reduced nuclei; 5, promycelium with nuclei in resting stage; 6, early and late anaphase stages; 7, mature promycelium with one nucleus in each cell; 8, 9, 10, 15 and 19, show young "knee joints" formed between adjacent cells; the formation of infection hyphae (the dicaryophase) has begun in several of them; also shown in some of the figures are simultaneous and separate migrations of the nuclei; 9, formation of infection hyphae between cells of the same promycelium by means of tube fusions; 11, 14 and 18, abnormal nuclear behavior or chromatic bodies of unknown sources; 14, the complete cross walls formed, in which is also shown abnormal chromatic bodies or abnormal nuclear behavior; 17, a four-celled promycelium, each nucleus in metaphase contains more than two chromosomes, or an unreduced number.

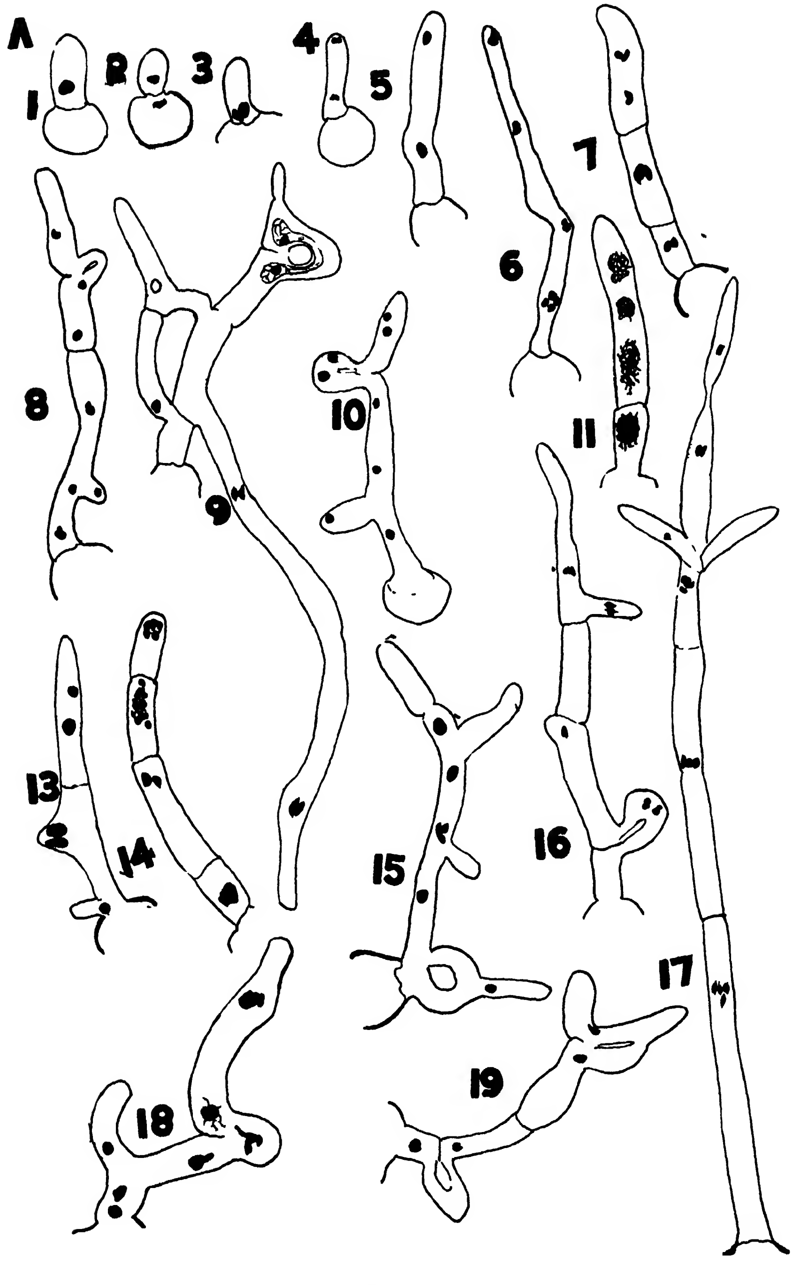

FIG. 2 A.

15, 16, 19). The "knee joints" represent the beginning of the dicaryophase and they soon develop large infection hyphae.

In the case of hyphae which originate by means of fusion of alternate cells, each cell produced a tube which soon becomes fused with a tube from another cell of the same promycelium, after which a

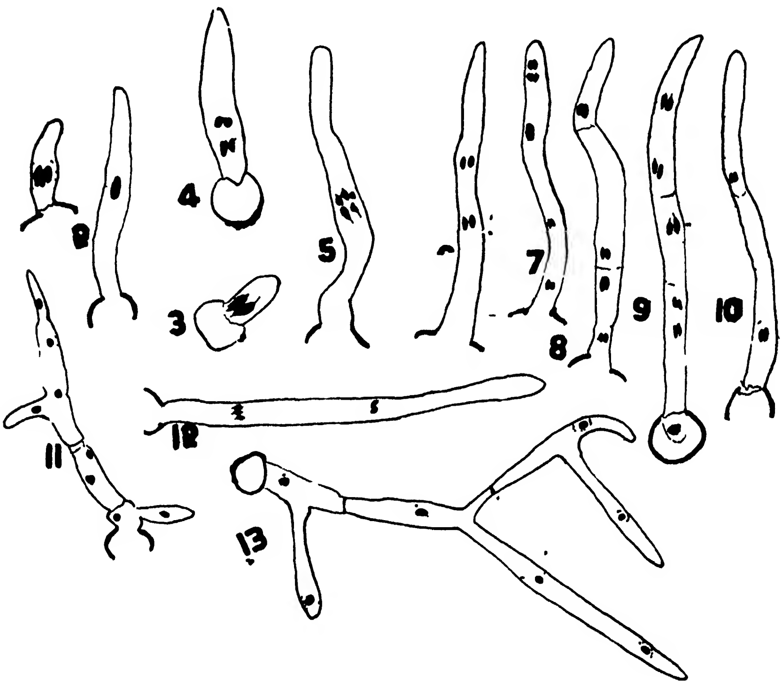

FIG. 2 B, *U. Spegazzinii* var. *agrestis*. Figs. 1 and 3, first metaphase stage in profile view; 2, resting nucleus; 4 and 6, early first anaphase, showing two chromosomes in each group; 5, early first anaphase stage with unequal distribution of chromosomes; 7–10, several telophase or late anaphase stages showing the beginning and completion of cell formation in the promycelium; 11, four promycelial cells with nuclei in the resting stage and young branches with nuclei in migration stages; 12, a promycelium with nuclei in second metaphase stage with different numbers of chromosomes; 13, promycelium branch with two conjugate nuclei and others in migrant stage.

large hypha containing two nuclei develops (FIG. 2 A: 9). In the same figure is shown a hypha containing two nuclei which originated from a cell without fusion.

Dark bodies of the type described for *U. Williamsii* were found in this species (FIG. 2 A: 11, 14, 18).

SOROSPORIUM CONSANGUINEUM Ellis & Ev.

Chlamydospores olivaceous, brown, irregularly polygonal, 7–10 μ diam.; epispore smooth. They begin to germinate after 9–12 hours in the incubator at 25° C. A tube emerges which elongates rapidly and in 3– 4 hours is completely developed, forming a 3–5 celled promycelium. Each promycelial cell bears one sporidium which sometimes forms secondary sporidia.

Nuclear behavior. Chlamydospores are uninucleate and diploid in the resting stage (FIG. 3: 1). When the spore germinates the young promycelium contains a deeply stained body which bears 4 or 5 chromatic elements; this appears to be the typical metaphase in profile and front view as shown in figure 3: 2, 3 and 4, respectively. Each one of these chromatic elements is prolonged by a thread so as to resemble a spindle. The promycelial tubes soon elongate and reduction division follows. Each group contains two chromosomes (FIG. 3: 5). The nuclei migrate toward the apex of the promycelium and at this stage the first promycelial wall is commonly produced (FIG. 3: 6). Apparently without a resting stage, these nuclei undergo a second division, such as that shown in figures 7 and 8. These illustrations represent what appears to be different anaphase stages. As soon as the nuclei are separated from each other, a wall forms between each pair and the promycelium becomes divided into cells (FIG. 3: 9, 10). These observations suggest that *S. consanguineum* possesses 4 chromosomes in the diploid stage and two in the haploid stage, and that the first division is reductional and the second equational. When division of the promycelium is complete, the nuclei undergo new equational divisions (FIG. 3: 10) just before sporidia are formed. One of the nuclei from each cell migrates into the sporidium and the other remains inside the promycelial cell. These divide again when new sporidia are formed.

The sporidia are soon separated from the promycelium and the nuclei divide again, sometimes two or three times, thus forming multinucleate sporidia (FIG. 3: 25). Worthy of note is one which seems to be near the last stage of nuclear division (FIG. 3: 25). Multinucleate sporidia are not common although Hanna (8) observed them in *S. Reilianum.*

Frequently spores of *S. consanguineum* germinated at low temperatures (8 to 10° C.), showed abnormalities in size in promycelium and nuclear behavior. These abnormalities were characterized by elongated promycelia, some of which were swollen cells, some with and some without cell formation. The nuclei of such promy-

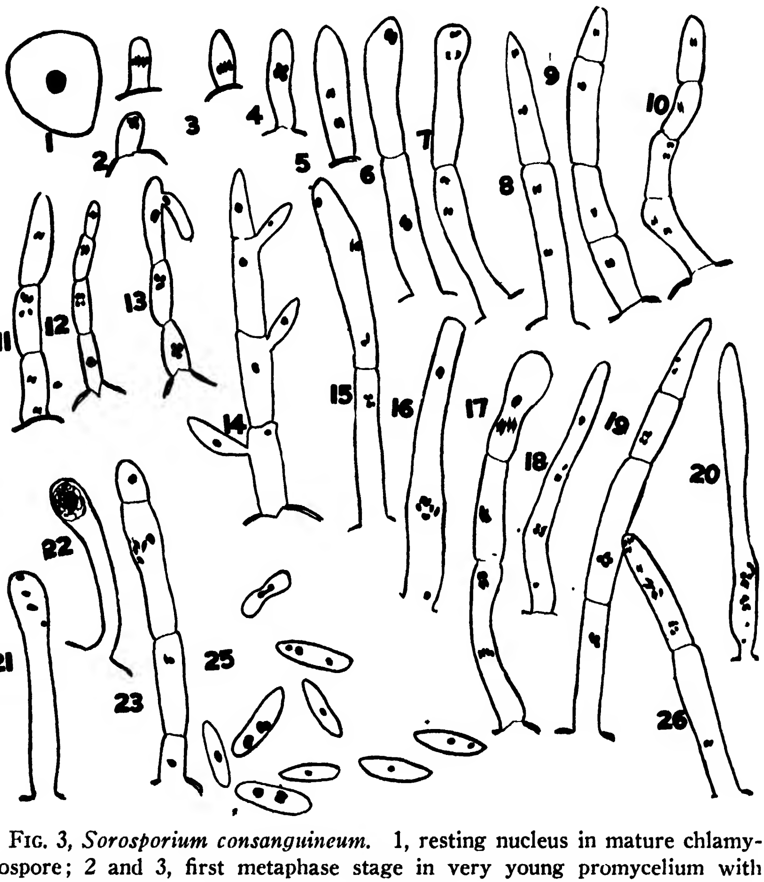

FIG. 3, *Sorosporium consanguineum.* 1, resting nucleus in mature chlamydospore; 2 and 3, first metaphase stage in very young promycelium with four chromosomes; 4, the same in front view; 5 and 6, early and late first anaphase stages with the number of chromosomes reduced to two in each group, first cross wall is shown in figure 6; 8, second anaphase stage; 9, late division stage showing mature promycelium; 10, equational division prior to sporidium formation; 11 and 13, nuclei in third division stage with a variable number of chromosomes in each group; 12, metaphase and anaphase stage, prior to sporidium formation; 14, sporidia developing from the promycelium following mitosis and the migration of one nucleus to each sporidium; 16–23 and 26, promycelia grown under low temperature showing abnormal development and nuclear behavior.

celia contained variable numbers of chromatic bodies. Figure 3: 11, 13, 16–23 and 26 illustrate these abnormalities.

DISCUSSION

It is known that segregation of factors for several characters occurs in the smuts either in the first, second, or later nuclear divisions in the promycelium (**5**, **6**, **11**, **16**, **17**, **18**). For the most part, the evidence that reduction occurs as late as the third division has been based on genetic studies, but Wang (**17**) has shown cytologically that reduction in *Ustilago Crameri* may occur also in the third division.

Evidence presented in this paper shows that reduction may occur in the third or later divisions in *U. Williamsii*, and that in *U. Spegazzinii*, var. *agrestis*, *U. halophila* and *Sorosporium consanguineum*, in the same promycelium there may be nuclei with variable numbers of chromosomes. However, in most cases the nuclei were reduced to 2 chromosomes before the formation of infection hypha or the sporidium. This was indicated by the fact that only a few remained with more than 2 chromosomes. Generally, therefore, the haploid number of chromosomes in these species is two. These apparently different types of chromosome reduction may be a source of different types of hyphae, and therefore of different biotypes.

As already pointed out, *U. Williamsii* produces three kinds of branches. One of these originates from a single promycelial cell and is haploid in nature. Consequently it cannot infect the host. Another kind originates from fused adjacent cells and has conjugate nuclei. This is a typical infection hypha. The third kind originates from a single promycelial cell and has only one nucleus which may be reduced for some characters but not for others. Therefore this kind may or may not be capable of infecting the host, depending upon whether reduction had occurred for sex. Thus, in its ability to produce this third kind of hypha *U. Williamsii* differs from other species which have been studied. Furthermore, it seems possible that hyphae of this type might represent "solopathogenic" lines, such as those found in *U. Zeae* (**2**).

In *U. Spegazzinii* var. *agrestis*, only two kinds of hyphae are produced, one of which develops from fused adjacent cells and the

other from individual cells. Both of these are binucleate but it could not be determined whether both kinds represent the dicaryophase. Infection hyphae, undoubtedly those which originate from single cells, are bisexual. On the other hand, those which originate from single cells may or may not represent the dicaryophase, depending upon whether the nucleus of the promycelial cell had been reduced for sex.

Hyphal formation in *U. halophila* is of two kinds, both of which are the product of fused promycelial cells. In one case the fusion is between adjacent cells by means of "knee joint" formations and in the other case fusion is between alternate cells by means of tubes. These differ, therefore, only in point of origin and both represent the dicaryophase.

Sporidial formation occurs occasionally in this species, in which case, fusion between sporidia or between mycelia produced by sporidia would precede the formation of infection hyphae. This process was not observed, however.

Sorosporium consanguineum differs from the other species studied, in that it produces sporidia instead of hyphae. Fusions between promycelial cells and between sporidia were not observed. The nuclear conditions of the sporidia while still attached to the promycelia indicated that they were haploid. In later stages the sporidia were largely multinucleate, probably as a result of nuclear divisions prior to budding. The absence of fusions probably was due to the fact that conditions were not favorable, since it seems logical that fusions may occur under natural conditions.

The significance of the abnormalities in the promycelium and in the nuclear behavior observed in *Sorosporium consanguineum* is not clear. It is known, however, that nuclear behavior in certain smut fungi is governed to some extent by environmental factors (**1**, **12**). In this case temperature seemed to exert a profound influence on type of germination and nuclear phenomena. The abnormal types usually appeared when the spores were germinated at a low temperature. In contrast, Wang (**17**) observed no influence of temperature on chromosome behavior in *U. Crameri.* This suggests, therefore, that different species may react differently to the same environmental factors.

The significance of the numerous darkly stained bodies of variable size and shape that were found in the promycelia of these species, along with nuclei that were in various stages of division, is not clear. They appeared to be chromatic in nature but the lack of uniformity in structure and behavior leaves one in doubt as to whether they actually are nuclear phenomena. Similar characters were referred to by D. T. Wang (**18**) as vacuomes and cytomes, which react to haematoxylin stain in the same manner as nuclei. On the other hand C. S. Wang (**17**) designated as nuclei, bodies of similar type in *U. Crameri*. Further studies with different staining and fixative methods will be necessary before definite conclusions can be drawn as to the nature of the bodies observed in the species studied. But in view of abnormalities due to unfavorable temperature, it may be suggested that unfavorable nutrient or other environmental factors were responsible for their appearance.

SUMMARY

1. Studies were conducted on the cytology of *Ustilago Williamsii, U. Spegazzinii* var. *agrestis, U. halophila,* and *Sorosporium consanguineum.*

2. The mature chlamydospores of *U. Williamsii* have a diploid nucleus. When the spore germinates the nucleus migrates to the promycelium where meiosis takes place. Apparently the diploid number of chromosomes is four. The reductional process may take place in the first, second, third or later nuclear divisions. In many cases primary and secondary hyphae possess unreduced nuclei. This is the first such case reported for smut fungi. In other cases it seemed there were hyphae in which reduction was complete for some chromosomes but not for others. Infection hyphae in this species develop by three means from the promycelial cells.

3. In *U. Spegazzinii* var. *agrestis* the mature chlamydospores contain one diploid nucleus. Except occasionally, when nuclear division apparently occurs inside the spore, the nucleus migrates to the promycelium where reduction division takes place. The diploid nuclei have four chromosomes. Two nuclei were observed in the late anaphase division stage. The first division on the promycelium is reductional but cases were observed in which it seemed that reduction did not take place in the first division. In this spe-

cies also, the promycelial cells developed into branched hyphae. These infection hyphae initiate the dicaryophase by means of nuclear migration from adjacent cells.

4. In *U. halophila* the mature chlamydospores are uninucleate and diploid. Nuclear division takes place in the promycelium, although in a few cases it was evident that division must have taken place inside the spore. The meiotic behavior was not clear, but in late stages of the second or third nuclear division it appeared that the haploid nuclei has 2 chromosomes. In some cases, nuclear reduction did not occur until sporidial or hyphal formation.

The infection hyphae may be originated by fusion between adjacent or alternate cells of the same promycelium. In the first case, this takes place by means of "knee joints" which seem to originate by elongation of promycelium membrane accompanied by the migration of the protoplasm and nuclei of the involucrate cells. This is followed by rupture and a partial projection of the membrane wall of the adjacent cells. The hyphae which originate as a result of fusion of alternate cells, do so when each cell elongates into a large tube which soon becomes fused with a tube from another cell of the same promycelium. After fusion is complete, a large hyphae develops, with nuclei from both cells. Uninucleate hyphae which formed from unfused cells also were observed.

5. In *Sorosporium consanguineum* the mature chlamydospore apparently possesses a diploid nucleus.

The meiotic process takes place in the promycelium. In the first division four chromosomes comprise the nucleus. In the second division it was possible to count only 2 in a group. Before sporidial formation the nucleus in the cell undergoes a new equational division and one nucleus migrates into the sporidium. The other remains inside the cell and sometimes divides again with the formation of additional sporidia. Sporidia with more than one nucleus were observed.

Low temperature seems to influence chromosome behavior during meiotic division resulting in unreduced nuclei and unequal distribution of chromosomes. Abnormalities in size and form of the promycelia were also produced.

The presence of many chromatic bodies of variable size and shape was observed in the four species studied.

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A CRITICAL STUDY OF SOME SPECIES OF USTILAGO CAUSING STEM SMUT ON VARIOUS GRASSES [1]

George W. Fischer and Elisa Hirschhorn [2]

(with 6 figures)

INTRODUCTION

The name *Ustilago hypodytes* (Schlecht.) Fries has long been associated with stem smut on many grasses, and in many parts of the world. The original description was by Schlechtendahl (Fl. Berol. 2: 129. 1824.) as *Caeoma hypodytes*. The type host is *Elymus arenarius* L., from Germany, but a large number of grasses have been reported as hosts since Fries recorded the species in the "Systema" (9).

During the course of a monographic study of the stem smuts of *Stipa* and *Oryzopsis* in North America (8), it was discovered that the binomial *Ustilago hypodytes* has for many years been applied to a complex of smut fungi, rather than to a single species. It is the purpose of this paper to present the results of a critical analysis of this complex, based on studies of hundreds of herbarium specimens from North America, South America, Europe, Asia, and Africa, most of which were identified as *U. hypodytes* by many prominent mycologists and issued as authentic exsiccati. Recent collections by the writers from North and South America are also included.

[1] Coöperative investigations of the smuts of forage grasses, by the Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture, and the Washington State Agricultural Experiment Station, Pullman, Washington. Published with the approval of the director as Scientific Paper No. 599.

[2] Pathologist, Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, and Assistant in Plant Pathology, State College of Washington, respectively.

The *Ustilago hypodytes* complex, as treated in this paper, embraces four species and one variety of smut fungi. These are separable into two groups: (1) Species whose spores possess bipolar areas or appendages; (2) Species whose spores lack bipolar areas or appendages.

I. STEM SMUT SPECIES WHOSE SPORES POSSESS BIPOLAR AREAS OR APPENDAGES

USTILAGO SPEGAZZINII Hirsch. Notas del Museo de la Plata, Botanica **4**: 415–419. 1939.
Ustilago hypodytes Auct.

Sori chiefly surrounding the internodes, but sometimes also involving more or less the inflorescence, although usually the inflorescence is entirely aborted, olive-brown to almost black, entirely naked except for the enveloping leaf sheaths; spores globose or sub-globose, to slightly oval or even somewhat angular, provided with bipolar sub-hyaline crests consisting of a prolongation of the epispore into a group of echinulations, finely papillose to minutely echinulate (oil immersion), clear yellowish-brown to olivaceous-brown, mostly 4–6 μ in diameter, or oval, 3.5–4 $\times$ 4–7 μ.

On GRAMINEAE:

Agropyron cristatum (L.) Gaertn. U. S.: Washington
Agropyron dasystachyum (Hook.) Scribn. U. S.: Washington
Agropyron inerme (Scribn. and Smith) Rydb. U. S.: Washington
Agropyron repens (L.) Beauv. U. S. Washington; Europe: Hungary, Spain, Germany, France; Africa: Tunis
Agropyron sibiricum (Willd.) Beauv. U. S.: Washington
Agropyron spicatum (Pursh) Scribn. U. S.: Washington
Agropyron trichophorum (Link) Richt. U. S.: Washington
Bromus erectus Hudson Europe: Germany
Elymus angustus Trin. ex Ledeb. U. S.: Washington
Elymus arenarius L. Europe: Germany
Elymus excelsus Turcz. U. S.: Washington
Elymus glaucus Buckl. U. S.: Washington
Melica Harfordii Boland. U. S.: Washington
Poa nevadensis Vasey U. S.: Washington

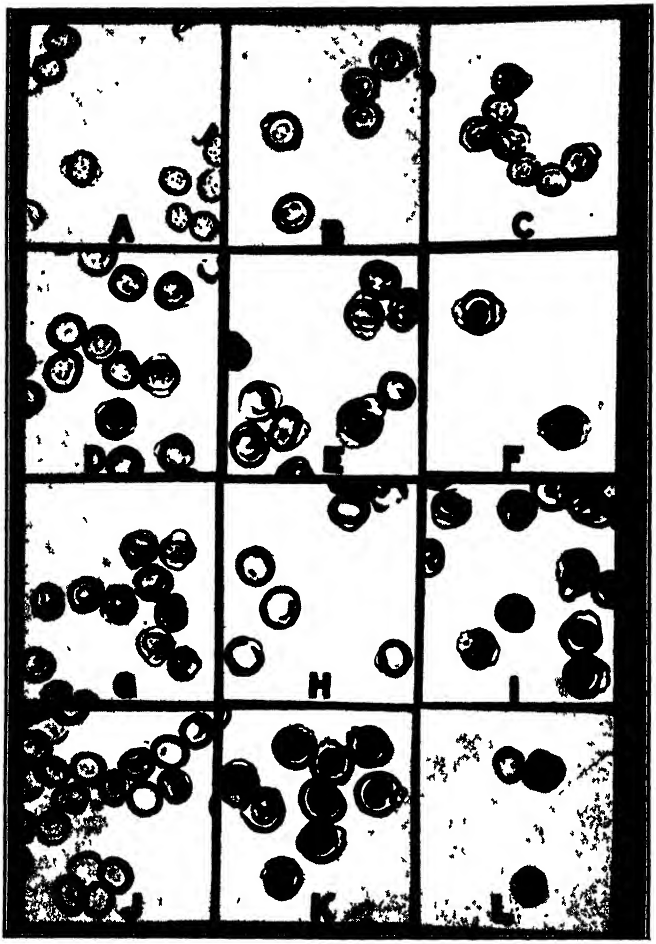

FIG. 1. A–C, *Ustilago Spegazzinii,* spores from: A, *Stipa Neesiana,* Argentin (loco typico); B, *Agropyron inerme,* United States; C, *Stipa Neesiana,* Bolivia; D–L, *Ustilago Spegazzinii* var. *agrestis,* spores from: D, *Agropyron rigidum,* Turkistan; E, *Lygeum spartum,* Sicily; F, *Stipa filiculmis,* Chile; G, *Agropyron acutum,* Italy; H, *A. repens,* Bohemia; I, *Bromus erectus,* Austria; J, *Elymus arenarius,* Sweden; K, *Lygeum spartum,* Spain; L, *Agropyron repens,* Germany (Sydow's *Ustilago agrestis*). All photomicrographs taken under same conditions of equipment, materials, lighting, and magnification. Somewhat retouched, to compensate where sharp focus is lacking. × approx. 800.

Poa palustris L. U. S.: Washington
Puccinellia distans (L.) Parl. U. S.: Washington
Sitanion hystrix (Nutt.) J. G. Sm. U. S.: California
Sitanion jubatum J. G. Sm. U. S.: Washington
Stipa mucronata HBK. (*S. setigera* Presl) Mexico
Stipa Neesiana Trin. and Rupr. South America: Bolivia, Argentina, Uruguay
Stipa robusta Scribn. (*S. vaseyi* Scribn.) U. S.: New Mexico
Stipa spartea Trin. U. S.: Illinois, Iowa, Wisconsin
Stipa viridula Trin. U. S.: N. Dakota, S. Dakota, Montana

During the course of these studies it has not been possible to refer to Schlechtendahl's original description of *Ustilago hypodytes*, nor has it been possible to obtain type material for study. Fries (9), in placing the species in the genus *Ustilago*, gives a description of macroscopic characters only. Thus it has been necessary to depend on mycological works subsequent to Fries' "Systema Mycologicum" for a description of the microscopic characters. In Table 1 is shown an analysis of the data given on the microscopic characters of *U. hypodytes* by twelve classical mycologists since Fries' time. The descriptions are strikingly similar. Of special importance is the fact that all these authors describe the epispore as *smooth*. Many of the specimens of *U. hypodytes* which we have studied are the same as those studied by some of the mycologists cited in Table 1. In the great majority of these specimens, on a wide variety of hosts, the spores have more or less the bipolar crests typical of *U. Spegazzinii*, either with or without the finely papillose epispore characteristic of the type material of the latter species. This observation applies to specimens representing the type host (*Elymus arenarius* L.) and the type locality (vicinity of Berlin, Germany) of *U. hypodytes*. Thus it is readily seen that (1) the presence of these characteristic crests has gone unrecognized or unheeded by numerous mycologists for several decades, and (2) apparently the name *Ustilago hypodytes* is a *nomen dubium*, under the provisions of Article 63, of the International Rules for Botanical Nomenclature. Only an examination of actual type material of *U. hypodytes* can positively verify these observations, but type material of this old species may no longer be available.

Three other species have been described since *Ustilago hypodytes,* as causing stem smut in various grasses and which have apparent similarities to *U. Spegazzinii,* both macroscopically and microscopically. These species are as follows:

Ustilago agrestis Syd. Ann. Myc. **22**: 278. 1924.
U. Bromi-erecti Cif. Ann. Myc. **29**: 51. 1931.
U. Stipae Cif. Ann. Myc. **29**: 52. 1931.

TABLE 1

TABULATION OF THE DATA GIVEN ON THE MICROSCOPIC CHARACTERS OF THE CHLAMYDOSPORES OF USTILAGO HYPODYTES BY VARIOUS MYCOLOGISTS

Author	Epispore	Dimensions	Color	Shape
Clinton (6)	smooth	4–7 μ in length		ovoid to spherical to irregular or polyhedral
McAlpine (14)	smooth	3–4 ×4–6 μ	dark olivaceous	globose to shortly ellipsoid
Migula (15)	smooth	3–4.5 ×3–6 μ	yellowish to olive brown	irregularly globose to slightly polyhedral
Ciferri (4)	smooth	4–5 or 4–5 ×3–6 μ	yellowish brown to olive brown	globose to ellipsoid
Liro (13)	smooth	3–5 ×4–6 μ	yellowish to brownish	more or less globose
Schellenberg (18)	smooth	3–5–7 μ	yellowish to brown	globose, ellipsoid or slightly angular
Saccardo (17)	smooth	3–4.5 ×3–6 μ	yellowish olive brown	globose, to ellipsoid, sometimes irregular to polyhedral
Plowright (16)	smooth	3–4.5 ×3–6 μ	yellowish brown	subglobose, oblong, or angular
Dietel (7)	smooth	4–5 μ	olive brown	globose
Winter (21)	smooth	3–5–6 μ	light brown	globose, irregularly globose, or polygonal
Lindau (12)	smooth	3–4.5 ×3–6 μ	yellowish olive brown	globose to irregularly ellipsoid
Bubak (3)	smooth	4–6, 7 μ	dark olive brown	globose to ovoid or angular

Although it has not been possible to examine type material of *Ustilago agrestis,* we have included subsequent material of this species identified by Sydow himself (Sydow, Mycotheca Germanica *2867*). Sydow (**20**) separated *U. agrestis* from *U. hypodytes* chiefly on the supposed specialization of the former to *Agropyron repens.* If Sydow observed the bipolar crests on the spores of his new species he made no mention of it in the species description, but the fact remains that the above-mentioned specimens have spores

which possess the bipolar crests and thus are very similar to other collections of stem smut on *A. repens* in the United States, Canada, Europe, and Africa.

Ciferri's (4) *Ustilago Bromi-erecti* is based on a biometric analysis of a collection of *U. hypodytes* on *Bromus erectus* Huds. from Austria. We have examined the same specimens (Zillig, Ustilag. Europ. No. 54) which Ciferri studied, and found the bipolar crests typical of *U. Spegazzinii.* However, Ciferri made no mention of these crests in his description of *U. Bromi-erecti.* The collection of stem smut on *B. erectus* on which Ciferri based his new species is very similar both macroscopically and microscopically to other collections of *U. hypodytes* on *B. erectus* from European countries. Both *U. agrestis* and *U. Bromi-erecti* have a smooth epispore.

Similarly, Ciferri (4) described *Ustilago Stipae* on a biometric basis, using two collections of *U. hypodytes* on *Stipa spartea* Trin. from the United States. We have included in our studies one of the two collections [3] forming the basis of Ciferri's "new" species. The spores of this collection have the bipolar crests and minutely echinulate epispore typical of *U. Spegazzinii.* Several other collections on *Stipa spartea* have the same characters. Ciferri made no mention in his description of *U. Stipae* of bipolar crests or of the minutely echinulate epispore.

From the above presentation it is seen that we have four binomials for this stem smut species which has bipolar crests on the spores, namely, *Ustilago agrestis, U. Bromi-erecti, U. Stipae,* and *U. Spegazzinii.* According to the descriptions, the first three species names have no connection with the principal diagnostic morphologic character, namely, the bipolar crests on their spores. It would appear, then, that these names are *nomina dubia.* The last name, *U. Spegazzinii,* is based on conspicuous morphological characters: bipolar crests on the spores and a minutely echinulate epispore.

Ustilago Spegazzinii was originally described (10) as occurring on *Stipa* only, and in Argentina. The results of the present studies show that many species of several other genera are also hosts, and in diverse parts of the world. On these hosts there is exhibited some variability in the morphology of the fungus. Thus it is pos-

[3] *U. hypodytes* on *Stipa spartea;* Meridian, Wisc., July 15, 1920, leg. J. J. Davis. Herb. Univ. Wisconsin.

sible to recognize, in the abundance of material examined, the following four groups:

Group I. Spores clear yellowish-brown, epispore minutely echinulate, crests comparatively inconspicuous, hyaline (FIG. 1, A).

Group II. Spores olivaceous-brown, epispore minutely echinulate, crests more or less inconspicuous, hyaline (FIG. 1, B and C).

Group III. Spores dark-brown, epispore finely papillose, crests more or less conspicuous, hyaline or concolorous (FIG. 1, D).

Group IV. Spores dark-brown; epispore *smooth*, crests variable, from inconspicuous bipolar entire thickened areas to conspicuous deeply dentate crests, hyaline (FIG. 1, E–L).

Of these four groups it is considered that the first two represent more or less typical *Ustilago Spegazzinii*. Group 3 differs from the typical *U. Spegazzinii* in having much darker spores, and with the epispore only slightly papillose. The fourth group is atypical with the smooth epispore, the variable crest, and dark color.

The third and fourth groups of *Ustilago Spegazzinii*, described above seem to comprise a distinct variety:

USTILAGO SPEGAZZINII var. **agrestis** (Syd.) comb. nov.

Spores dark-brown, smooth or very finely papillose (under oil immersion), crests varying from entire apical thickenings to conspicuous, deeply dentate crests, sub-hyaline to concolorous with the spore.

On GRAMINEAE:

Agropyron acutum (DC.) Roem. & Schult. Europe: Italy
Agropyron amurense Drobov U. S.: Washington (= *A. pendulinum* (Nevski) Swall.)
Agropyron cristatum (L.) Gaertn. U. S.: Washington
Agropyron elongatum (Host.) Beauv. U. S.: Washington
Agropyron glaucum Roem. & Schult. Europe: Switzerland (= *A. intermedium* (Host) Beauv.)

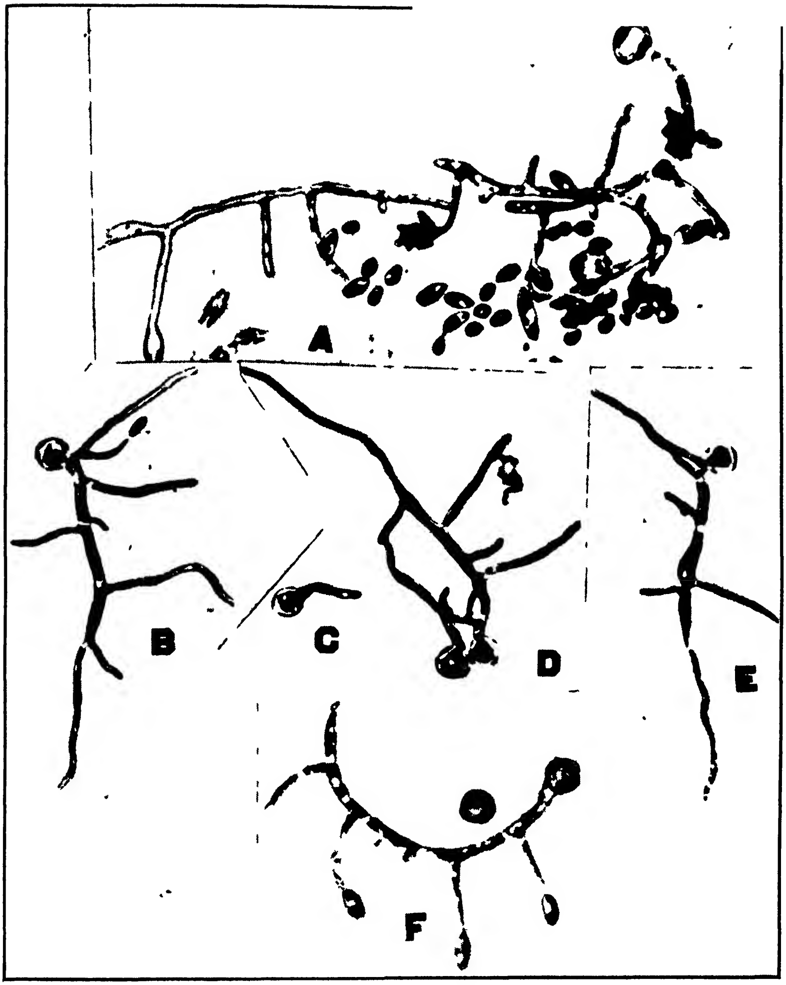

FIG. 2. A–E, germinating spores of *Ustilago Spegazzinii* var. *agrestis;* A, advanced germination, showing production of aerial sporidia, from *Agropyron Smithii,* Pullman, Wash.; B–E, ibid., from *A. intermedium,* Pullman, Wash., showing earlier stages of germination. Near spore in (E) a fusion has occurred from which an infection hypha is developing; F, germinating spore of *U. Spegazzinii,* showing production of sporidia, from *A. spicatum,* Goldendale, Wash. All spores germinated on malt extract-dextrose-peptone agar and stained *in situ* with cotton blue and lactophenol. All photographed under same conditions of light, apparatus, and magnification. Somewhat retouched, to compensate where sharp focus is lacking. × approx. 800.

Agropyron inerme (Scribn. & Smith) Rydb. U. S.: Washington
Agropyron intermedium (Host.) Beauv. Europe: Italy
Agropyron junceum (L.) Beauv. Europe: Great Britain
Agropyron Smithii Rydb. U. S.: Washington, Montana, Colorado
Agropyron spicatum (Pursh) Scribn. U. S.: Washington
Agropyron trachycaulum (Link) Richt. U. S.: Washington
Agropyron repens (L.) Beauv. U. S.: Washington, New York; Canada: Ontario, Sask., B. C.; Africa, Tunis; Europe: Spain
Agropyron rigidum (Schrad.) Beauv. Asia: Turkestan
Agropyron semicostatum (Steud.) Nees U. S.: Washington
Bromus erectus Huds. Europe: Germany, Switzerland, France
Elymus arenarius L. Europe: Germany, Scandinavia
Elymus canadensis L. U. S.: Washington
Elymus condensatus Presl U. S.: Washington, Utah
Elymus dahuricus Turcz. U. S.: Washington
Elymus striatus L. U. S.: Montana
Lygeum spartum Loef. ex L. Europe: Spain, Italy; Africa: Algeria
Poa ampla Merr. U. S.: Washington
Poa scabrella (Thurb.) Benth. U. S.: Nevada
Sitanion Hansenii (Scribn.) J. S. Sm. U. S.: California
Sitanion hystrix (Nutt.) J. G. Sm. U. S.: California
Stipa californica Merr. & Davy U. S.: California, Mt. Shasta
Stipa filiculmis Delile South America: Chile
Stipa mucronata HBK. (*S. setigera* Presl) Mexico: Coronado Isl.
Stipa pulchra Hitchc. U. S.: California
Stipa spartea Trin. U. S.: Illinois
Stipa viridula Trin. U. S.: N. Dakota
Stipa sp. South America: Argentina

Group I is considered typical of *Ustilago Spegazzinii*. Group II is a color variation, with the spores being darker and less clear. These differences are relatively insignificant, and are merely recog-

nized as possibly indicating different forms only. The same applies to the differences between Groups III and IV. With a very few exceptions, all the collections studied have been readily classified in one of the four groups. For instance, one collection on *Stipa filiculmis* has the epispore and crest characters typical of *U. Spegazzinii,* but also the color of the variety *agrestis.* In another case, a collection on *Poa ampla* appears to be a mixture of *U. Spegazzinii* and the variety *agrestis.*

GEOGRAPHIC DISTRIBUTION

Ustilago Spegazzinii and the variety *agrestis* do not seem to be entirely co-existent. *U. Spegazzinii* has the following distribution, based upon the specimens we have examined: North and South America, central and southern Europe, and North Africa. The variety *agrestis* is represented in North and South America, Scandinavia, northern central and southern Europe, central Asia, North Africa. Furthermore, the variety appears to be more abundant than the species. In the United States, especially at Pullman, Washington, both the species and the variety (more especially the latter) are more or less common on several exotic grasses [4] including such species as *Agropyron amurense, A. cristatum, A. elongatum, A. junceum, A. rigidum, A. semicostatum, A. sibiricum, A. trichophorum, Elymus angustus,* and *E. dahuricus.* Of these, *A. cristatum* (crested wheat-grass) is commonly observed with 5–25 per cent infection in large fields planted for seed production, forage, or soil conservation. It is a matter of interesting conjecture as to the source of these infections. It seems possible that local perennial heavy infestations (25–95 per cent) on *A. repens* could represent one or more races capable of attacking these exotic species. Data are lacking concerning the actual importance of this stem smut elsewhere, except that in Argentina the junior author has observed as high as 25 per cent infection in *Stipa Neesiana* and *Stipa* sp.

[4] These grasses are planted in the extensive observational row nurseries of the Soil Conservation Service, Division of Nurseries, and the Forage Crops Nursery of the Bureau of Plant Industry, Soils and Agricultural Engineering, U. S. Dept. of Agriculture.

Other authors, Liro (13), Bornhövd (2), Ciferri (4), *et al.* cite many species in several other genera as hosts to *Ustilago hypodytes.* Doubtless many of these should be listed as hosts to *U. Spegazzinii* and the variety *agrestis,* but it is impossible to determine which, because at the present time specimens are not available supporting these citations.

Likewise, other mycologists list several synonyms under *Ustilago hypodytes.* It has not been possible to examine type material representing these binomials, but it is suspected that some of these may be associated with *U. Spegazzinii* and *U. Spegazzinii* var. *agrestis.*

SPECIMENS STUDIED

CANADA: On *Agropyron repens,* Saskatoon, Sask., 6–16–38, leg. and fid. R. C. Russel, Univ. Toronto Crypt. Herb. No. *638; ibid.,* Wilcox Lake, Ont., 6–14–36, leg. R. F. Cain, fid. H. S. Jackson, Univ. Toronto Crypt. Herb. No. *9553; ibid.,* Toronto, Ont., 6–8–36, leg. H. S. J. and R. F. Cain, fid. H. S. Jackson, Univ. Toronto Crypt. Herb. No. *9554; ibid.,* Toronto, Ont., 6–22–34, leg. H. S. Jackson, fid. H. S. J., Univ. Toronto Crypt. Herb. No. *6700; ibid.,* Westboro, Ont., 8–18–35, leg. M. Timonin, fid. ?, Univ. Toronto Crypt. Herb. No. *9827; ibid.,* Vineland, Ont., 6–9–39, leg. Richardson and McKeen, fid. H. S. Jackson, Univ. Toronto Crypt. Herb. No. *16122; ibid.,* Kleinburg, Ont., 9–8–35, leg. G. D. Darker, fid. H. S. Jackson, Univ. Toronto Crypt. Herb. No. *10200;* on *A. trachycaulum,* Summerland, B. C., 8–10–40, leg. M. F. Welch, fid. M. F. W. and H. S. Jackson.

UNITED STATES: On *Agropyron amurense,* Pullman, Wash. (S. C. S. Nursery),[5] 7–26–43, leg. E. Kreizinger, fid. G. W. Fischer, No. *329,* Myc. Coll. Bur. Pl. Ind. No. *85184;* on *A. cristatum,* Pullman, Wash., 6–21–37, leg. and fid. G. W. Fischer, No. *148,* Myc. Coll. Bur. Pl. Ind. No. *85004; ibid.,* Goldendale, Wash., 6–23–43, leg. and fid. G. W. Fischer, No. *322,* Myc. Coll. Bur. Pl. Ind. No. *85117; ibid.,* Pullman, Wash., 7–26–43, leg. and fid.

[5] Many of the collections from Pullman, Wash. have come from the forage nurseries at this station. Those from the Soil Conservation Service nurseries are indicated as "S.C.S. Nursery"; those from the Bureau of Plant Industry are indicated as "B.P.I. Nursery."

G. W. Fischer, No. *335,* Myc. Coll. Bur. Pl. Ind. No. *85190;* on *A. dasystachyum,* Pullman, Wash. (B. P. I. Nursery), June 1943, leg. and fid. G. W. Fischer; on *A. elongatum,* Pullman, Wash. (S. C. S. Nursery), 6–19–40, leg. and fid. G. W. Fischer, No. *149,* Myc. Coll. Bur. Pl. Ind. No. *85005;* on *A. inerme,* Pullman, Wash., 6–21–37, leg. and fid. G. W. Fischer, No. *145,* Myc. Coll. Bur. Pl. Ind. No. *85001; ibid.,* La Crosse, Wash., 6–21–43, leg. and fid. G. W. Fischer, No. *336,* Myc. Coll. Bur. Pl. Ind. No. *85191;* ibid., Prosser, Wash., 6–24–43, leg. and fid. G. W. Fischer, No. *330,* Myc. Coll. Bur. Pl. Ind. No. *85158;* on *A. intermedium,* Pullman, Wash. (B. P. I. Nursery), 7–26–43, leg. E. Kreizinger, and fid. G. W. Fischer, No. *332,* Myc. Coll. Bur. Pl. Ind. No. *85192;* on *A. repens,* Pullman, Wash., June 1937, leg. and fid. G. W. Fischer; *ibid.,* Colfax, Wash., July, 1940, leg. J. F. Schafer, fid. G. W. Fischer, No. *171,* Myc. Coll. Bur. Pl. Ind. No. *85027; ibid.,* Hall, N. Y., 7–9–23, leg. Martin and Haskell, fid. V. K. Charles, Myc. Coll. Bur. Pl. Ind.; on *A. semicostatum,* Pullman, Wash. (S. C. S. Nursery), June 1939, leg. and fid. G. W. Fischer, No. *166,* Myc. Coll. Bur. Pl. Ind. No. *85022;* on *A. sibiricum,* Pullman, Wash. (S. C. S. Nursery), 6–24–38, leg. and fid. G. W. Fischer, No. *168,* Myc. Coll. Bur. Pl. Ind. No. *85024;* on *A. Smithii,* Billings, Mont., July 1900, leg. Griffiths and Large, David Griffiths, West American Fungi, No. *234; ibid.,* La Jara, Colo., 8–14–1900, leg. and fid. C. L. Shear, No. *983,* Myc. Coll. Bur. Pl. Ind.; *ibid.,* Pullman, Wash. (B. P. I. Nursery), 6–24–38, leg. and fid. G. W. Fischer, No. *167,* Myc. Coll. Bur. Pl. Ind. No. *85023; ibid.,* 7–26–43, Pullman, Wash. (B. P. I. Nursery), leg. and fid. G. W. Fischer, No. *356,* Myc. Coll. Bur. Pl. Ind. No. *85210;* on *A. Smithii* var. *molle* Jones, Bozeman, Mont., 7–6–35, leg. H. A. Rodenhiser, fid. G. W. Fischer, No. *146,* Myc. Coll. Bur. Pl. Ind. *85002;* on *A. spicatum,* Pullman, Wash. (S. C. S. Nursery), 6–24–38, leg. and fid. G. W. Fischer, No. *165,* Myc. Coll. Bur. Pl. Ind. No. *85021; ibid.,* 7–2–43, leg. and fid. G. W. Fischer, Myc. Coll. Bur. Pl. Ind.; *ibid.,* Roosevelt, Wash., 6–23–43, leg. Fischer, Law, and Menzies, fid. G. W. Fischer, No. *339,* Myc. Coll. Bur. Pl. Ind. No. *85194;* on *A. trachycaulum,* Pullman, Wash., 7–2–36, leg. and fid. G. W. Fischer, No. *164,* Myc. Coll.

Bur. Pl. Ind. No. *85020; ibid.,* 7–24–43, leg. and fid. G. W. Fischer, No. *338,* Myc. Coll. Bur. Pl. Ind. No. *85193;* on *A. trichophorum,* Pullman, Wash. (B. P. I. Nursery), 7–3–40, leg. and fid. G. W. Fischer, No. *170,* Myc. Coll. Bur. Pl. Ind. No. *85026; ibid.,* Pullman, Wash. (S. C. S. Increase Plot), 7–2–43, leg. and fid. G. W. Fischer, No. *340,* Myc. Coll. Bur. Pl. Ind. No. *85195;* on *Elymus angustus,* Pullman, Wash. (S. C. S. Nursery), June 1939, leg. and fid. G. W. Fischer; on *E. canadensis,* Pullman, Wash. (S. C. S. Nursery), 7–16–40, leg. J. L. Schwendiman, fid. G. W. Fischer, No. *169,* Myc. Coll. Bur. Pl. Ind. No. *85025; ibid.,* 7–26–43, leg. and fid. G. W. Fischer, No. *332,* Myc. Coll. Bur. Pl. Ind. No. *85187;* on *E. condensatus,* Murray, Utah, Sept. 1918, leg. W. W. Jones, fid. A. O. Garret; *ibid.,* Dusty, Wash., 6–26–40, leg. and fid. G. W. Fischer, No. *150,* Myc. Coll. Bur. Pl. Ind. No. *85006;* on *E. dahuricus,* Pullman, Wash., 7–26–43, leg. E. Kreizinger, fid. G. W. Fischer, No. *331,* Myc. Coll. Bur. Pl. Ind. No. *85186;* on *E. glaucus,* Pullman, Wash. (S. C. S. Nursery), 6–24–38, leg. and fid. G. W. Fischer, No. 161, Myc. Coll. Bur. Pl. Ind. No. *85007;* on *E. striatus,* Billings, Mont., Aug. 1900, leg. Griffiths and Large, David Griffiths, West American Fungi, No. *201;* on *Melica Harfordii,* Pullman, Wash. (S. C. S. Nursery), June 1939, leg. and fid. G. W. Fischer, No. *163,* Myc. Coll. Bur. Pl. Ind. No. *85019;* on *Poa ampla,* Pullman, Wash. (S. C. S. Nursery), June, 1939, leg. and fid. G. W. Fischer, No. *162,* Myc. Coll. Bur. Pl. Ind. No. *85018; ibid.,* Pullman, Wash. (B. P. I. Nursery), 7–22–43, leg. and fid. G. W. Fischer, No. *342,* Myc. Coll. Bur. Pl. Ind. No. *85197;* on *P. scabrella* (Thurb.) Benth. (*P. buckleyana* Nash), Rabbit Hole, Nev., Aug. 1902, leg. and fid. D. Griffiths, No. *176,* Myc. Coll. Bur. Pl. Ind.; on *P. nevadensis,* Pullman, Wash. (S. C. S. Nursery), June 1938, leg. and fid. G. W. Fischer, No. *160,* Myc. Coll. Bur. Pl. Ind. No. *85016; ibid.,* June 1939, leg. and fid. G. W. Fischer, No. *159,* Myc. Coll. Bur. Pl. Ind. No. *85015; ibid.,* 6–14–40, leg. and fid. G. W. Fischer, No. *158,* Myc. Coll. Bur. Pl. Ind. No. *85014;* on *P. palustris,* Pullman, Wash. (S. C. S. Nursery), June 1939, leg. and fid. G. W. Fischer, No. *157,* Myc. Coll. Bur. Pl. Ind. No. *85013; ibid.,* June 1940, leg. and fid. G. W. Fischer, No. *156,* Myc. Coll. Bur. Pl. Ind. No. *85012;* on

Puccinellia distans, Pullman, Wash. (S. C. S. Nursery), 6–19–40, leg. and fid. G. W. Fischer, No. *155*, Myc. Coll. Bur. Pl. Ind. No. *85011;* on *Sitanion Hansenii,* vic. Mt. Shasta, Calif., 7–21–39, leg. W. B. Cooke, fid. B. L. Zundel, Cooke, Mycobiota of North America, No. *58;* on *S. hystrix,* vic. Mt. Shasta, Calif., 9–17–39, leg. W. B. Cooke, fid. G. L. Zundel, Cooke, Mycobiota of North America, No. *62; ibid.,* 8–20–39, leg. W. B. Cooke, fid. G. L. Zundel, Cooke, Mycobiota of North America, No. *59;* on *S. jubatum,* Pullman, Wash. (S. C. S. Nursery), June 1939, leg. and fid. G. W. Fischer, No. *152,* Myc. Coll. Bur. Pl. Ind. No. *85008;* on *Stipa occidentalis* Thurb., vic. Mt. Shasta, Calif., 8–22–39, leg. W. B. Cooke, fid. G. L. Zundel, Cooke, Mycobiota of North America, No. *61;* on *S. spartea,* Scatterwood, S. Dak., July, 1896, leg. D. Griffiths, Ex. Herb. David Griffiths, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Urbana, Ill., 6–21–88, leg. M. B. Waiter, fid. G. P. Clinton, Seymour and Earle, Economic Fungi, Supp., No. *C71; ibid.,* Grinnell, Iowa, 6–9–05, leg. B. Fink, fid. W. W. Diehl, Myc. Coll. Bur. Pl. Ind.; *ibid.,* Highmore, S. Dak., leg. G. R. Ball, fid. E. E. Dicks, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Meridian, Wisc., 7–18–20, leg. J. J. Davis, ex Herb. Univ. Wisc. (No. *19696* Herb. James R. Weir); on *S. robusta* (*S. vaseyi*), Paton Mts., N. Mex., 8–18–03, leg. and fid. D. Griffiths, No. *251,* Herb. Brooklyn Bot. Gard.; on *S. viridula,* Aberdeen, S. Dak., July 1895, ex Herb. D. Griffiths, Myc. Coll. Bur. Pl. Ind.; *ibid.,* Billings, Mont., 7–12–00, leg. Griffiths and Lange, fid. D. Griffiths, No. *252,* Herb. Brooklyn Bot. Gard.; *ibid.,* Morrison, Colo., 6–10–05, leg. E. Bethel, "Reliquiae Bethelianae," Myc. Coll. Bur. Pl. Ind.; *ibid.,* Manfred, N. Dak., 8–2–22, leg. Gilman Shirley, Brenckles' Fungi Dakotensis, No. *524; ibid.,* Sprague Siding, Minn., 6–3–41, leg. R. Sprague, fid. G. W. Fischer, No. *186,* Myc. Coll. Bur. Pl. Ind. *85042.*

MEXICO: On *Stipa mucronata* (*S. setigera*), Coronado Isl., 7–8–15, Elam Bartholomew's Fungi Columbiani, No. *4794.*

ARGENTINA: On *Stipa Neesiana,* La Plata, 1939, leg. and fid. E. Hirschhorn; on *Stipa* sp., Neugen, 2–1940, leg. and fid. E. Hirschhorn, No. *709.*

BOLIVIA: On *Stipa Neesiana,* Coleapirue, Feb. 1940, leg. M. Gardenas, No. *26A,* fid. J. A. Stevenson, Myc. Coll. Bur. Pl. Ind.

CHILE: On *Stipa filiculmis,* Freire, Dec. 1928, leg. Bro. Claude Joseph, No. *5818,* fid. J. A. Stevenson and A. J. Watson, Myc. Coll. Bur. Pl. Ind.

URUGUAY: On *Stipa Neesiana,* 1943, leg. B. Rosengurtt, fid. E. Hirschhorn, No. *1093.*

TURKESTAN: On *Agropyron rigidum,* Samarkand, July 1910, leg. Serebrianikow, Tranzschel et Serbrianjkow Myco-theca Rossica, No. *203.*

SWEDEN: On *Elymus arenarius,* 7–30–87, leg. C. J. Johanson, fid. Eriksson, Fungi Parisitici Scandinavia, No. *251; ibid.,* Sept. 1890, Varberg. Fungi Scandinavia, No. *1641; ibid.,* Scania, Aug. 1896, leg. G. Lagerheim, Vestergren Micromycetes rariores selecti, No. *391.*

ENGLAND: On *Elymus arenarius,* 1891, leg. Plowright, issued as Sydow Ustilagineen, No. *10;* on *Agropyron junceum,* near Liverpool, 3–8–97, leg. P. Magnus, issued as Vestergren Micromycetes rariores selecti, No. *1595.*

GERMANY: On *Agropyron repens,* Thuringen Erfurt, 6–26–04, leg. H. Diedicke, issued as Sydow, Mycotheca Germanica, No. *217; ibid.,* Berlin, June, 1896, leg. P. Sydow, issued as Sydow, Ustilagineen, No. *106; ibid.,* pr. Islebiam (Sax. Bor.), June, 1875, leg. and fid. J. Kunze, issued as Johs. Kunze, Fungi selecti exsiccati, No. *15; ibid.,* Lunderaberg in Mähren, June 1924, leg. R. Picbauer, issued as F. Petrak, Flora Bohemiae et Moraviae exsiccata, No. *1988; ibid.,* Hessen-Nassau; Geisenheim a Rh., 7–6–22, leg. G. Lüstner, issued as Zillig, Ustilagineen Europas, No. *23; ibid.,* Reuhof, 1894, issued as Herbier Barbey-Boissier, No. *1832;* on *Elymus arenarius,* Pommern: bei Zingst, 14–8–12, leg. P. Sydow, Sydow, Mycotheca germanica, No. *1164; ibid.,* Berlin, 10–1893, leg. P. Sydow, Sydow Ustilagineen, No. *10; ibid.,* Hazelhorst, 23–8–12, leg. and fid. A. Ludwig, Herb. Dr. A. Ludwig; *ibid.,* VII, 1895, ex. Herb. P. Magnus, Flora Pomeranica, No. 253; *ibid.,* Pommern, Kreis Usedorn-Wollin: Stranddünen bei Misdroy, 3–9–25, leg. Dr. Martin Noak, issued as Zillig's Ustilagineen Europas, No. *24.*

AUSTRIA: On *Bromus erectus,* Haschberg bei Klosterneuburg, 7–1925, leg. Dr. K. Keissler, issued as Zillig's Ustilagineen Europas, No. *54.*

BOHEMIA: On *Agropyron repens,* Ziegelschanke ad Trebritz, 25–7–00, by Fr. Bubak, issued as Vestergren's Micromycetes rar. selecti, No *334.*

HUNGARY: On *Agropyron repens,* Budapest, June 1883, issued as Linhart, Fungi hungarici, No. *104*

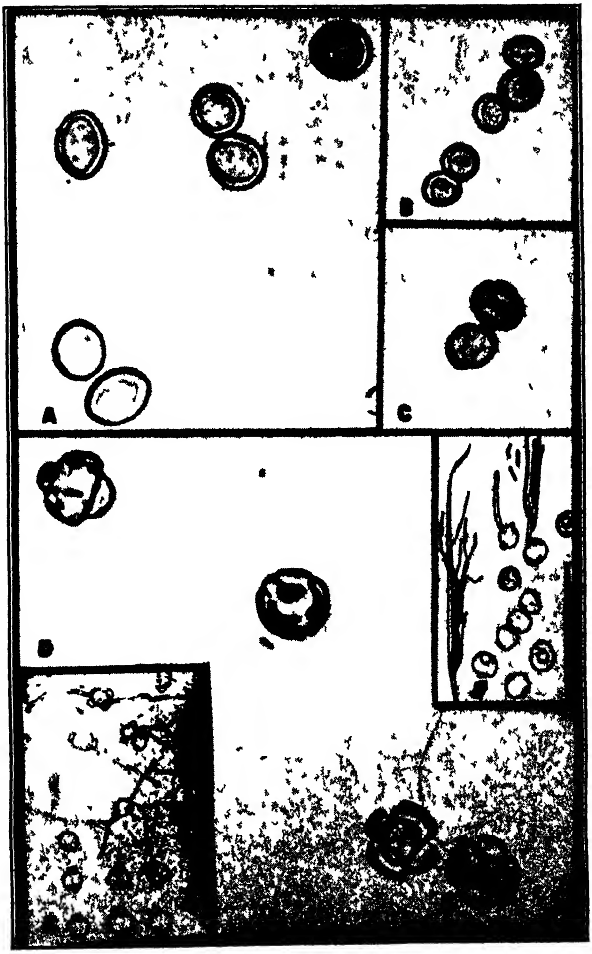

FIG. 3 A, *Ustilago halophila,* chlamydospores, type material; B, *U. nummularia,* chlamydospores, type material, C, *U. Williamsii,* chlamydospores, from Argentine specimen, D, *ibid.,* type material, from U. S., E, Spegazzini's original illustrations of type material of *U appendiculata* (*U Williamsii*) after Hirschhorn; F, Lavrov's original illustrations of *Transchiella otophora* (*U. Williamsii*), after Zundel. A–D, × approx. 1000.

FRANCE: On *Agropyron repens,* Route de la Gare, Grignon, 3–6–35, Herb. G. Viennot-Bourgin, Flore cryptogamique de Seine-et-Oise: on *Bromus erectus,* Grignon, 20–VII–35, *ibid.*

SWITZERLAND: On *Agropyron glaucum,* Pris de Stalden, Vallu de St. Canton du Valais, July 26, 1914, leg. Dr. Eng. Mayor; on *A. intermedium,* Canton du Valais, 7–6–11, leg. E. Mayor, issued as Sydow, Ustilagineen, No. *452* and as Vestergren, Micromycetes rariores selecti, No. *1595 a;* on *Bromus erectus,* Canton de Neuchatel, 6–18–23, leg. Eug. Mayor.

ITALY: On *Agropyron acutum,* Rovigno, June 1902, leg. P. Sydow, issued as Sydow, Ustilagineen, No. *307;* on (?) *Lygeum spartium* (host not named), Cagliari, 1900, Briosi e Cavara Ustilaginee, No. *376;* on (? host not named), Briosi e Cavara Ustilaginee, No. *228.*

SPAIN: On *Lygeum spartum,* Casterlseras, leg. Loscos, issued as Rabenhorst, Fungi Europaei, No. *1800;* on *Agropyron repens,* Oredo, VII, 1919, Herb. del Museo Nacional de Ciencias Naturales de Madrid, No. *13081.*

SICILY: On *Lygeum spartum,* 1877, leg. V. Beltrani, issued as de Thuemen, Mycotheca Universalis, No. *930.*

ALGERIA: On *Lygeum spartum,* 4–18–06, leg. Rene Maire, issued as Vestergren, Micromycetes rariores selecti, No. *1205; ibid.,* Oran, 4-11–06, leg. R. Maire, issued as Sydow, Ustilagineen, No. *361.*

TUNIS: On *Agropyron repens,* Rossitz Morav., leg. Niessl, in Myc. Coll. Bur. Pl. Ind.

SPORE GERMINATION IN USTILAGO SPEGAZZINII AND U. SPEGAZZINII VAR. AGRESTIS

Hirschhorn (*10*) observed only 3 germinated spores in her studies of *Ustilago Spegazzinii* and provisionally described germination as follows:

"Las clamidosporas germinan en agua a 25° C. approximadamente, produciendo un promicelio 2–4 celular, con una esporidia en cada celulua."

On the basis of numerous observations of germinating spores of recent specimens (collected in United States) of *Ustilago Spegaz-*

zinii and *U. Spegazzinii* var. *agrestis* the process of spore germination may be briefly described as follows: On plain or nutrient agar, and at room temperature (20–22° C.), germination does not commence until after 40 hrs. or more. A single germ tube emerges (FIG. 2, C), elongates, and usually soon becomes differentiated more or less into a 3–4 celled promycelium. However, these cells have not been observed to produce primary sporidia, but instead long slender branches (FIG. 2, B, D, E). Occasionally a sporidium will be formed at the tip of one or more of these branches (FIG. 2, F) but more often the branches elongate and rebranch, to initiate a mycelium. Very soon aerial branches begin to bear chains of aerial sporidia (FIG. 2, A). Fusions have been noted between detached aerial sporidia.

USTILAGO WILLIAMSII (Griff.) Lavrov. Trav. Inst. Sci. Biol. Univ. Tomsk. **2**: 22. 1936.

Ustilago hypodytes Auct.

Sorosporium Williamsii Griff. Bull. Torrey Club **29**: 296. 1902.

Ustilago appendiculata Speg. Anal. Museo. Nac. De Buenos Aires III. **12**: 288. 1909.

Tranzschiella otophora Lavrov. Trav. Inst. Sci. Biol. Univ. Tomsk. **2**: 29. 1936.

Sori surrounding the upper internodes, often involving also remnants of the aborted inflorescence, dark-brown to black, naked except for the enclosing leaf sheaths; spores globose to sub-globose, provided with an exospore that is smooth but deeply cracked, and bearing two bipolar cap-like appendages (sometimes four), dark olivaceous-brown, 7–10 μ in diameter.

On GRAMINEAE:

Oryzopsis Bloomeri (Boland.) Ricker U. S.: Washington

Oryzopsis hymenoides (Roem. and Shult. Ricker. U. S.: Montana, Wyoming

Stipa californica Merr. and Davy U. S.: California

Stipa cernua Stebbins and Love U. S.: California

Stipa comata Trin. and Rupr. U. S.: Oregon, Montana

Stipa coronata Thurb. U. S.: California

Stipa humilis Cav. (*S. chrysophylla* Desv.) South America: Argentina

Stipa Lettermani Vasey U. S.: Wyoming
Stipa occidentalis Thurb. U. S.: California, Oregon
Stipa Richardsoni Link U. S.: Montana, Wyoming

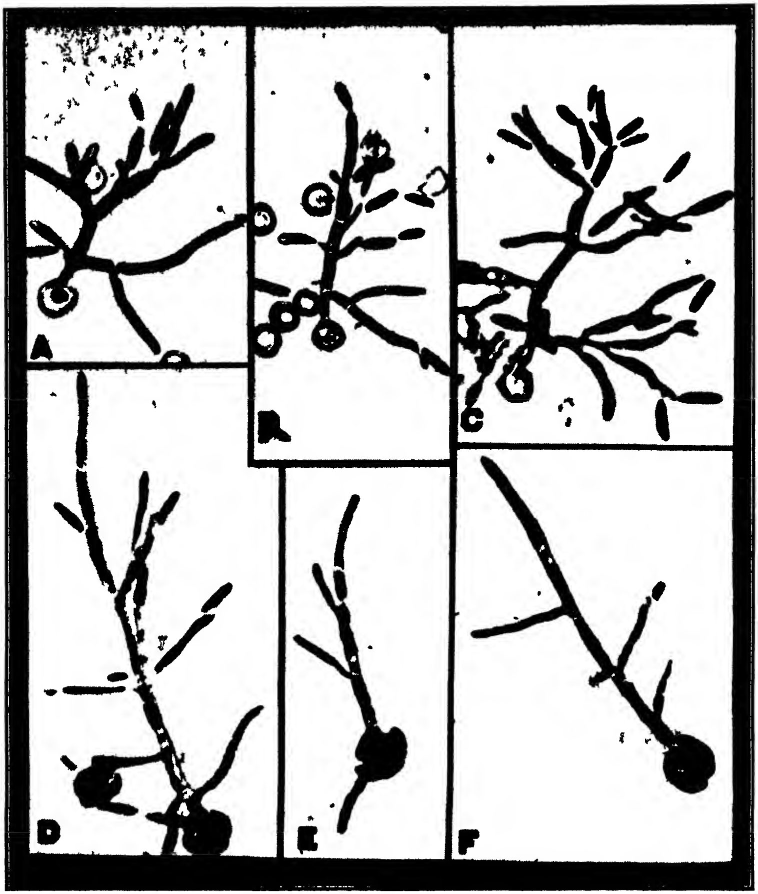

FIG. 4. A–C, *Ustilago halophila,* germinating spores, showing sporidial production; D–F, *U. Williamsii,* germinating spores. Germinated on malt extract-dextrose agar, and stained *in situ* with cotton blue in lacto-phenol × approx. 800.

Stipa speciosa Trin. and Rupr. U. S.: California
Stipa Thurberiana Piper. U. S.: Washington, Oregon
Stipa viridula Trin. U. S.: Montana
Stipa sp. U. S.: California; South America: Argentina

Of the above list of host species, all except *Stipa humilis* (*S. chrysophylla*) and *S. Richardsoni* are new hosts.

A comparison of type material of *Ustilago appendiculata* (in Herb. Instituto de Botanica Spegazzini No. *3004,* Argentina, Mendoza, Cacheuta, Feb. 1909) and *Sorosporium Williamsii* (David Griffiths, West American Fungi No. *306* on *Stipa Richardsonii,* Big Horn Mts., Wyo., Col. Williams and Griffiths, Aug. 1898) leaves no doubt as to their identity. However, we do not consider this species as a *Sorosporium,* thus concurring with Clinton's (**5**) opinion that the "spore balls" of Griffith's species "result from a mechanical adherence of the spores in irregular masses." Since Griffiths' specific epithet has several years priority over that of Spegazzini we are proposing the new combination shown above. It is regrettable that the specific name *"appendiculata"* can not be conserved, because it is descriptive of the chief diagnostic character of this smut.

Recently Lavrov, according to Zundel (**22**), described a new genus of the Ustilaginaceae, *Tranzschiella,* the type species of which is *T. otophora* Lavrov, on *Stipa* in Siberia. According to the descriptions and illustrations of this species which Zundel (**22**) reproduced, it appears to be very similar to *U. Williamsii* and we are considering the two as synonymous, provisionally, until examination of type material makes a permanent disposition possible. Reproductions of Lavrov's illustrations of *T. otophora* and of Spegazzini's illustration of *U. appendiculata* are presented with our own of *Ustilago Williamsii* (FIG. 3, C, D, E, F) to show the apparent identity. The size and color of the spores, the appendaged or cracked character of the epispore, and the characters of germination are very strikingly similar. Hirschhorn (**11**) considered that *U. appendiculata* did not merit generic distinction because (1) the characters of spore germination are quite typical of *Ustilago;* (2) the sori are composed of a free, powdery or granular mass, as in most species of *Ustilago,* and (3) the presence of appendages on the spores is not sufficient in itself. The appendages of the spores of this smut are a character of the epispore. If such a character is accepted as a valid foundation for a new genus, then also a reticulate epispore could form the basis for a new genus, or such a

species as *U. Spegazzinii* with its characteristic bipolar prolongations of the epispore would equally merit generic distinction.

There are some variations in the character of the epispore of *Ustilago Williamsii* on different hosts in the U. S. that deserve mention. On some species of *Stipa* the spores are clear and yellowish, while on other species the spores are dark brown and opaque. In some specimens the epispore is deeply cracked to form the outlines of the appendages but these are largely lacking. In other collections portions of the cracked epispore have separated sufficiently to form conspicuous appendages.

SPECIMENS EXAMINED: ARGENTINA: Type material, *U. appendiculata* on *Stipa humilis* (*S. chrysophylla*), Herb. Instituto de Botanica Spegazzini No. *3004.* Mendoza, Cacheuta, Feb. 1909; on *Stipa* sp., leg. and fid. E. Hirschhorn, Mar. 1940, Hirschhorn Herb. No. *685.*

UNITED STATES: On *Oryzopsis Bloomeri,* Pullman, Wash. (S. C. S. Nursery), June 1940, leg. and fid. G. W. Fischer, No. *180,* Myc. Coll. Bur. Pl. Ind. No. *85036;* on *O. hymenoides,* Drummond, Mont., July 17, 1941, leg. Fischer and J. R. Hardison, fid. G. W. Fischer, No. *194,* Myc. Coll. Bur. Pl. Ind. No. *85050; ibid.,* Pinedale, Wyo., 7–23–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *204,* Myc. Coll. Bur. Pl. Ind. No. *85060;* on *Stipa californica,* Mt. Shasta, Calif., Cooke, Mycobiota of North America, No. *60,* fid. G. L. Zundel, 9–17–38; on *S. cernua,* Davis, Calif., leg. Stebbins and Love, fid. G. W. Fischer, No. *198,* Myc. Coll. Bur. Pl. Ind. No. *85054;* on *S. comata,* Big Timber, Mont., 7–19–41, leg. Fischer and J. R. Hardison, fid. G. W. Fischer, No. *195,* Myc. Coll. Bur. Pl. Ind. *85051; ibid.,* Billings, Mont., 7–19–41, leg. Fischer and J. R. Hardison, fid. G. W. Fischer, No. *197,* Myc. Coll. Bur. Pl. Ind. No. *85053; ibid.,* Demi, Ore., 8–1–01, Col. D. Griffiths (no. 249), Herb. Brooklyn Bot. Gard.; on *S. coronata,* Monrovia, Calif., leg. and fid. E. Bethel, Reliq. Bethelianae in Myc. Coll. Bur. Pl. Ind.; on *S. Lettermani,* Moran, Wyo., 7–22–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *200,* Myc. Coll. Bur. Pl. Ind. No. *85056; ibid.,* Triangle F Ranch, Wyo., 7–23–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *202,* Myc. Coll. Bur. Pl. Ind. No.

85058; on *S. occidentalis,* Ingo Nat. Forest, Calif., 8–5–25, leg. W. W. Wagener, fid. W W. Diehl, Myc. Coll. Bur. Pl. Ind.; *ibid.,* Steins Mts., Ore., 1901, Griffiths, W. Amer. Fungi; on *S. Richardsoni,* Yellowstone Pk., Wyo., 7–21–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *199,* Myc. Coll. Bur. Pl. Ind. No. *85055; ibid.,* Butte, Mont., 7–18–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *203,* Myc. Coll. Bur. Pl. Ind. No. *85059; ibid.,* Big Horn Mts., Wyo., 1898, Griffith's West Amer. Fungi, No. *306* (type material of *Sorosporium* (*Ustilago*) *Williamsii*); on *S. speciosa,* Palmdale, Calif., 5–24–41, leg. H. W. Johnson, fid. G. W. Fischer, No. *212,* Myc. Coll. Bur. Pl. Ind. No. *85068; ibid.,* Banning, Calif., Griffith's W. Amer. Fungi, No. *250,* 5–14–06, in Herb. Brooklyn Bot. Gard.; *ibid.,* Mono Lake, Calif., 7–30–22, Reliq. Bethelianae, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Coll. Griffiths and Hunter, Griffiths Coll. No. *47* in Herb. Brooklyn Bot. Garden; on *S. Thurberiana,* Prosser, Wash., 6–24–43, leg. Fischer, Law, and Menzies, fid. G. W. Fischer, No. *348,* Myc. Coll. Bur. Pl. Ind. No. *85202; ibid.,* Pullman, Wash. (in forage plots), June, 1940, leg. and fid. G. W. Fischer, No. *181,* Myc. Coll. Bur. Pl. Ind. No. *85037; ibid.,* Mabton, Wash., 6–21–43, leg. Fischer, Law, and Menzies, fid. G. W. Fischer, No. *193,* Myc. Coll. Bur. Pl. Ind. No. *85049; ibid.,* between Goldendale and Toppenish, Wash., 6–23–43, leg. Menzies, Law, and Fischer, fid. G. W. Fischer, No. *347,* Myc. Coll. Bur. Pl. Ind. No. *85201;* on *Stipa viridula,* McLeod, Mont., 7–19–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *205,* Myc. Coll. Bur. Pl. Ind. No. *85061;* on *Stipa* sp., Pigeon Pass, Box Springs Mts., Calif., 6–3–31, leg. W. T. Horne, fid. H. B. Humphrey, A. G. Johnson, and W. W. Diehl, Myc. Coll. Bur. Pl. Ind.; on *Stipa* sp., Caliente, Calif., D. Griffiths Coll. No. 410, 7–22–04, Herb. Brooklyn Bot. Gard.; on *Stipa* sp., Laguna Mts., Calif., 7–20–20, Rel. Bethelianae, in Myc. Coll. Bur. Pl. Ind.; on *Stipa* sp., Lebec, Calif., 1920, Reliq. Bethelianae, fid. R. W. Davidson, in Myc. Coll. Bur. Pl. Ind.

SPORE GERMINATION IN USTILAGO WILLIAMSII

In our experience, the spores of *Ustilago Williamsii* germinate readily, on a variety of media. On malt extract-dextrose-peptone

agar, germination begins in four or five hours at room temperature. A rather slender promycelium emerges from one of the appendaged areas, and soon develops two or three cross-walls. From each of the cells thus formed a primary sporidium or a branch develops, as in figure 4, D and F. When only two cross-walls are formed three cells result in the promycelium, and the spore itself acts as the fourth cell, in which case a branch or sporidium usually emerges from the appendaged area opposite the promycelium (FIG. 4, E).

II. STEM SMUT SPECIES WHOSE SPORES LACK BIPOLAR AREAS OR APPENDAGES

In this category are treated two species of *Ustilago* in the *U. hypodytes* complex, whose spores are smooth and completely lack any bipolar areas or appendages.[6] Until now these species have been identified as *U. hypodytes*. We consider them to belong to two species not hitherto recognized as occurring in the United States.

USTILAGO HALOPHILA Speg. Anal. Museo. Nac. Buenos Aires III. 1: 58. 1902.

Ustilago hypodytes Auct.

Cintractia Distichlidis McAlp. Smuts of Australia, p. 169, Melbourne, 1910.

Sori surrounding the internodes and the rachis of the aborted inflorescence, enclosed at first by a thin grayish membrane (the host epidermis),[7] dark-brown to black, granular to pulverulent. Spores globose, ovoid, to slightly irregular, yellow or yellowish-brown to olivaceous-brown, smooth, chiefly 5–7 μ in diameter, or 4–6 × 7–8 μ (FIG. 3, A).

[6] *Ustilago minima* Arth. on *Stipa* and *Oryzopsis* has small smooth spores and superficially resembles the *U. hypodytes* complex. However, the sori are covered by a distinct and usually persistent membrane, and the species is therefore considered wholly unrelated to the other species herein treated.

[7] Spegazzini in his original description (7) makes no mention of a membrane around the sorus, but the type material plainly possesses it. We have found the membrane in all of the specimens of "*Ustilago hypodytes*" on *Distichlis* spp. examined. For this reason we have included mention of the membrane in the description of *U. halophila* above.

FIG. 5. *Ustilago halophila*. A, type material, on *Distichlis spicata* (Herb. Inst. Speg. No. 3198), illustrating the dwarfing effect; B, on *D. stricta*, without dwarfing effect, Salt Lake City, Utah, Fischer Coll. No. 173; C, McAlpine's *Cintractia Distichlidis* (*U. halophila*), to show similarity to elongate, American specimens; D, *U. halophila* on *Distichlis* sp. with dwarfing effect, Roswell, N. Mexico, Herb. D. Griffiths. Somewhat reduced.

On GRAMINEAE:

Distichlis spp.[8] U. S.: Idaho, New Mexico, Nevada, California, Washington, Arizona, Utah; South America, Argentina; Australia

The stem smut on *Distichlis* spp. common in the western states has been considered, until now, as *Ustilago hypodytes*. In Argentina, Spegazzini (**19**) described in 1902 a stem smut of *Distichlis spicata* (L.) Greene as *U. halophila*. We have studied type material of this species and are convinced that the stem smut of *Distichlis* in the United States is identical with it.

McAlpine (**14**) gave the name *Cintractia Distichlidis* to a stem smut attacking *Distichlis spicata* in Australia. We have not had the opportunity of examining type material of McAlpine's species, but his adequate description and excellent illustrations leave no doubt as to its identity with Spegazzini's *U. halophila* and with "*U. hypodytes*" on *Distichlis* in the United States.

Among the specimens examined during the present studies we have noticed three types of smutted plants of *Distichlis* spp. One is quite dwarfed (FIG. 5, A and D) and another is considerably taller (FIG. 5, B). A third type is intermediate between the two extremes. On the dwarf type the sori seem to be more or less confined to the last internode and the rachis of the aborted inflorescence. In the taller type the sori occupy several internodes. The spore characters are the same in both types and it is our opinion that the smut species is the same in both. Spegazzini's *Ustilago halophila* represents the "dwarfed" type (FIG. 5, A) and McAlpine's *Cintractia Distichlidis* apparently represents the taller type (FIG. 5, C) although he mentions that the host is sometimes much reduced in size due to the fungus (**6**). We are inclined to give no more significance to these three types than that they may represent three types of host species, not three types of smut. Clinton (**2**) states that *Distichlis maritima* Raf. (a synonym for *D. spicata* is sometimes very much dwarfed by stem smut.

[8] The hosts are given here as *Distichlis* spp. because it is our opinion that among the specimens we have examined there are some instances where the host species has been incorrectly determined; this also in view of Beetle's (**1**) recent demonstration of variation in the common species, *D. spicata*.

SPORE GERMINATION IN USTILAGO HALOPHILA

Spore germination in *Ustilago halophila* has been observed in recent collections from Washington and Utah. On dextrose malt extract agar, after 18–24 hours at room temperature (21–22° C.)

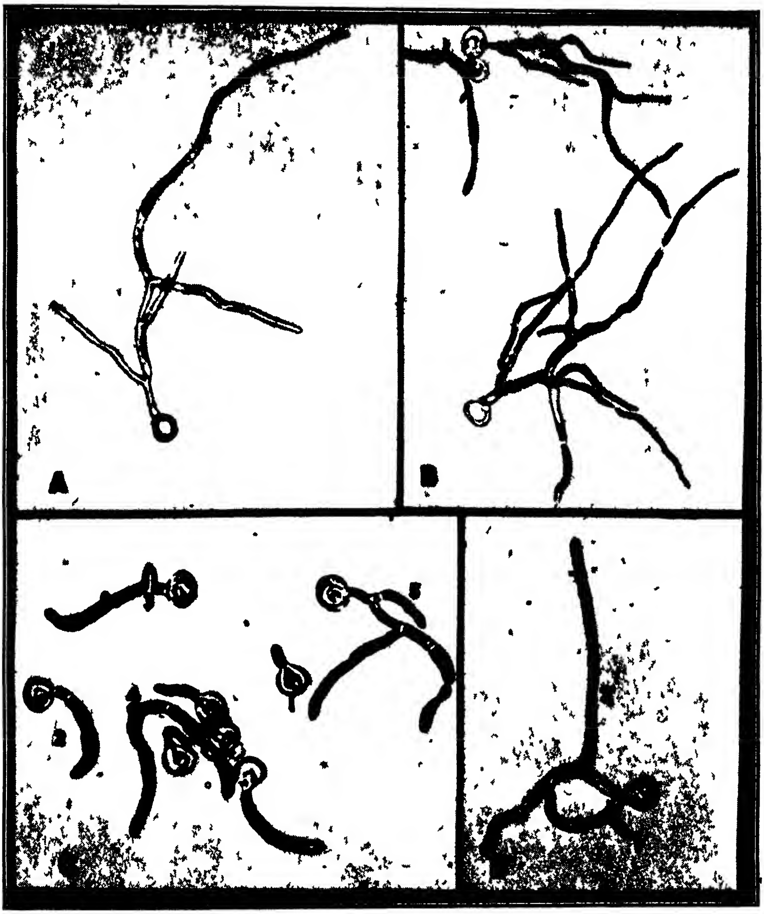

FIG. 6. A, B, *Ustilago nummularia*, germinating spores; C, *U halophila*, germinating spores, fusions between adjacent cells are seen at 3 and 4, at 5 is a fusion tube from cell no. 1 about to contact and fuse with cell no. 3; D. *ibid.*, two infection hyphae developing from same promycelium; at 2 the infection hypha appears to have developed from the point of fusion between adjacent cells, at 1 the infection hypha is developing from the copulation tube connecting two remote cells (nos. 1 and 4). Germinated on malt extract dextrose agar and stained *in situ* with cotton blue in lactophenol. × approx. 800.

a germ tube begins to emerge from the spore (FIG. 6, C, 1). This elongates rather rapidly and soon becomes septate (FIG. 6, C, 2). Sometimes fusions occur between the cells of the promycelium (FIG. 6, C, 3 and 4). These fusions quickly give rise to infection hyphae (FIG. 6, D, 1 and 2). More often sporidia are borne from the promycelial cells or from branches of the promycelium (FIG. 4, A–C). This account comprises the first published description of spore germination in *U. halophila.*

SPECIMENS EXAMINED

ARGENTINA: Santa Fe; Rufino, Mar. 1900, Herb. Inst. Speg. No. *3198* (Type material) on *Distichlis spicata.* U. S.: Washington; Grant Co., on *Distichlis stricta* (Torr.) Rydb. col. D. C. Smith and J. R. Swallen, July 1940, fid. G. W. Fischer, No. *174,* Myc. Coll. Bur. Pl. Ind. No. *85030;* Blue Lake, on *D. stricta* 9–10–40, leg. and fid. G. W. Fischer, No. *357,* Myc. Coll. Bur. Pl. Ind. *85211;* Utah: Salt Lake City, on *D. stricta,* 7–16–40, col. G. W. Fischer, No. *123,* Myc. Coll. Bur. Pl. Ind. No. *85029;* Salt Lake City, on *D. stricta,* 8–24–14, A. O. Garret Herb. No. *2272;* Arizona: Empire Ranch, on *D. spicata,* leg. D. Griffiths, No. *174,* Herb. Brooklyn Bot. Gard.; New Mexico: Roswell, on *D. spicata,* 9–5–03, Vesterg. Micromycetes, No. *898* (Griffiths No. *205* in Herb. Brooklyn Bot. Gard.). Nevada: Quinn River Crossing, on *D. spicata,* 6–19–01, Herb. D. Griffiths, No. *235;* California Monterey, on *D. spicata,* Feb. 1910, leg., M. S. Clemens; Idaho: Roberts, on *D. spicata,* Aug. 1917, leg. F. S. Walpert, ex. Herb. James R. Weir, No. *8990.*

USTILAGO NUMMULARIA Speg. Anal. Museo. Buenos Aires III. **1**: 59. 1902.

Ustilago hypodytes Auct.

Sori surrounding the internodes and sometimes extending into the aborted inflorescence, enclosed at first by the leaf sheaths, dusty, dark brown to almost black; spores globose to sub-globose, yellowish, brown, or olivaceous, smooth, chiefly 4–5 μ in diameter, or 3–4 × 4–5 μ.

On GRAMINEAE:

Ammophila arenaria (L.) Link Europe: Latvia

Ammophila arundinacea Host (Synonym of *A. arenaria*) Europe: Germany

Oryzopsis hymenoides (Roem. and Schult.) Ricker United States: Washington, Idaho, Utah, Colorado, Montana, Wyoming

Stipa comata Trin. & Rupr. United States: California, Oregon, Washington, Wyoming, Montana

Stipa neomexicana Thurb. & Scribn. United States: New Mexico

Stipa speciosa Trin. & Rupr. South America: Argentina

Stipa sp. United States: California

Of the above list of host species, all but *Stipa speciosa* must be considered as new host species to *Ustilago nummularia.*

The stem smuts of *Stipa* and *Oryzopsis* in North America having naked sori and small (4–7 μ), smooth spores without bipolar areas correspond to the various descriptions of *Ustilago hypodytes.* However, since we can not be certain as to the exact nature of the species to which this binomial was first given it becomes necessary to consider other names. Spegazzini in 1902 (7) described *U. nummularia* on *Stipa speciosa* in Argentina. An examination of type material of this species has revealed the identity of the North American stem smuts in question to Spegazzini's species.

SPORE GERMINATION IN USTILAGO NUMMULARIA

Germination has not been observed to begin in less than 2 days after sowing the spores on malt extract dextrose agar and incubation at room temperature (18–19° C.). A slender, hyaline germ tube emerges which develops rather rapidly, with sparse branching. Often the promycelium becomes 4-celled and from each cell a branch protrudes as though primary sporidia were in the process of development in the classic fashion of sporidia-producing smuts, but these protuberances merely develop into branches, as seen in figure 6, A. These continue to elongate and in turn branch (FIG. 6, B) and this process gives rise to a rapidly growing mycelium. Neither aerial nor surface-born sporidia have been observed.

SPECIMENS EXAMINED

UNITED STATES: on *Oryzopsis hymenoides,* Provo, Utah, leg. and fid. A. O. Garrett, No. *3129a; ibid.,* Near Edwin Natural Bridge, San Juan Co., Utah, 8–3–11, leg. and fid. A. O. Garrett, No. *2224; ibid.,* Emery Co., Utah, leg. and fid. A. O. Garrett; *ibid.,* San Juan Co., Utah, 7–22–11, leg. and fid. A. O. Garrett, No. *2178; ibid.,* Orondo, Wash., 8–11–26, leg. Zundel and Zentner, fid. G. L. Zundel; *ibid.,* Wolcott, Colo., 7–27–98, leg. D. S. Shear, fid. R. W. Davidson, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Glenwood Springs, Colo., 7–26–98, leg. Shear and Bessey, fid. R. W. Davidson, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Connel, Wash., 6–28–22, leg. and fid. George L. Zundel, Ustillaginales of the United States, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Orondo, Wash., 8–11–26, leg. G. L. Zundel and F. H. Zientner, fid. G. L. Zundel; Ustilaginales of the United States in Myc. Coll. Bur. Pl. Ind.; *ibid.,* St. Anthony, Idaho, Aug. 1900, leg. E. D. Merrill, fid. R. W. Davidson, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Glenwood Spa, Colo., 7–29–98, leg. C. L. Shear, fid. R. W. Davidson, in Myc. Coll. Bur. Pl. Ind.; *ibid,* Flockert's Ranch, Wyo., 6–30–01, leg. E. D. Merrill and E. N. Wilcox, No. *1197;* fid. J. C. Arthur, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Lind, Wash. (branch Exp. Sta.), *7–20–37,* leg. and fid. G. W. Fischer, No. *176,* in Myc. Coll. Bur. Pl. Ind. No. *85032; ibid.,* Shelley, Idaho, Aug. 1937, leg. D. C. Smith, fid. G. W. Fischer, No. *177,* in Myc. Coll. Bur. Pl. Ind. No. *85033; ibid.,* Pinedale, Wyo., 7–23–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *188,* in Myc. Coll. Bur. Pl. Ind. No. *85044; ibid.,* Pullman, Wash. (S. C. S. Nurs.), 7–10–41, leg. and fid. G. W. Fischer, No. *196,* Myc. Coll. Bur. Pl. Ind. No. *85052;* on *Stipa comata,* Northville, S. Dak., 7–18–29, leg. and fid. J. F. Brenckle; Fungi Dakotenses, No. *675; ibid.,* Lakeside, Calif., 7–18–13, leg. E. Bethel, Reliquiae Bethelianae, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Woodward, Okla., 8–31–40, leg. C. L. Lefebvre, fid. G. W. Fischer, Myc. Coll. Bur. Pl. Ind. No. *85043; ibid.,* Moro, Ore., 7–17–35, leg. Virgil Hawk, fid. G. W. Fischer, No. *174,* Myc. Coll. Bur. Pl. Ind. No. *85031; ibid.,* Cody, Wyo., 7–20–41, leg. Fischer and Hardison, fid. G. W. Fischer, No. *192,* in Myc. Coll. Bur. Pl. Ind. No. *85048; ibid.,*

Pasco, Wash., 6-24-43, leg. A. G. Law and G. W. Fischer, fid. G. W. Fischer, No. *354,* Myc. Coll. Bur. Pl. Ind. No. *85208;* on *Stipa neomexicana,* Santa Fe, New Mexico, 8-23-26, leg. Bros. G. Arsene and A. Benedict, fid. G. P. Clinton and G. L. Zundel, in Myc. Coll. Bur. Pl. Ind.; on *Stipa* sp. (no host given on packet), Nevada City, Calif. July 1926, leg. L. S. Smith, fid. G. L. Zundel; Ustilaginales of the U. S., in Myc. Coll. Bur. Pl. Ind.

CANADA: On *Oryzopsis hymenoides,* Beaver Creek, Sask., 8-28-38, leg. T. Stevenson, fid. R. C. Russel, No. *711* in Univ. of Toronto Crypt. Herb.

ARGENTINA: On *Stipa speciosa* (Type material), La Plata, 1900, leg. Spegazzini, in Herb. Inst. Speg. d. Bot. No. *3619.*

LATVIA: On *Ammophila arenaria,* Düna, 16-VII-1903, leg. F. Bucholtz, ex Herb. Inst. Phytopath. Univ. Tartuensis.

GERMANY: On *Ammophila arundinacea* (synonym of *A. arenaria*), Berlin, 1876, leg. P. Sydow, issued as de Thuemen, Mycotheca Universalis, No. *820.*

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PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XXXIX. A NEW HELOTIUM

Fred J. Seaver

(with 1 figure)

In November 1938, the writer received from Mr. Maurice Walters of Cleveland, Ohio, a rather unusual cup-fungus. In form it resembled a minute *Cudonia* but did not fit any of the plants described for this genus, either in consistency or in size, being much too minute.

It was finally decided, on more critical examination, that it was a stipitate *Helotium* in which the apothecium soon became convex and *Cudonia*-like. However, because of the uncertainty of its identity it was not published, although the illustrations had been prepared.

In October 1944, H. M. Fitzpatrick sent specimens collected by one of his students, Mr. Richard P. Korf, in Ithaca, which are identical with those sent from Cleveland. This has prompted me to publish the illustrations made several years ago with records and descriptions. Since the fungus resembles in form species of *Cudonia* it is described under the following name:

Helotium cudonioides sp. nov.

Apotheciis stipitatis, gregariis, vel caespitosis dein convexis 2 mm. diam., brunneis; stipitis albidis vel pallidis, 2–3 mm. long., vix 1 mm. diam.; ascis clavatis 8-sporis, 100 μ long., 10–12 μ diam.; sporiis subdistichis, fusoideis, hyalinis 5×16–$20\ \mu$; paraphysibus filiformibus, 1 mm. diam.

Apothecia stipitate, single or cespitose, at first concave, soon becoming strongly convex, reaching a diameter of 2 mm., pale to dark brown; stem white or nearly white, reaching a length of 2–3 mm. and less than 1 mm. in diameter; asci clavate, 8-spored reaching a length of 100 μ and a diameter of 10–12 μ; spores 1-seriate below and irregularly 2-seriate above, fusoid, hyaline, about 5×16–$20\ \mu$; paraphyses filiform, 1 mm. or less in diameter.

FIG. 1. *Helotium cudonioides.*

On rotten wood.

Type locality: Cleveland, Ohio.

Distribution: New York and Ohio.

NEW YORK BOTANICAL GARDEN

EXPLANATION OF FIGURE

Lower, photograph of a group of apothecia on rotten wood about 2½ times enlarged; above, drawings of three apothecia in different stages and from different angles; left, ascus with spores and paraphysis and two spores freed; right, empty ascus showing ascostome.

NOTES AND BRIEF ARTICLES

Apparent Allies of Amanita verna

The spores of *A. verna* are globose. Species that resemble it macroscopically are *A. bisporigera, A. hygroscopica, A. virosa, A. magnivelaris, A. gemmata volvata,* etc. In Florida a number of species in this genus have elongate spores, and these species curiously enough exhibit lines of evolution similar to those with globose or ellipsoid spores. The two here described, for example, might be mistaken for *A. verna* when fresh but their spores are elongate.

Venenarius margarita sp. nov.

Pileo convexo-plano, 5–6.5 cm. lato, albido, grato; lamellis liberis, confertis, albis; sporis oblongis, 10–11 × 3–4 μ; stipite albo, floccoso, 8 × 1–1.3 cm.; bulbo magno, albo; volva ampla, 2 cm. lata; annulo magno, albo.

Pileus convex to plane, scattered, 5–6.5 cm. broad; surface slightly viscid when wet, smooth, glabrous, dull-white with an avellaneous tint, pearly when dry, slightly yellowish on the disk, sometimes with one or two volval patches, margin even, entire; context very thin, white, unchanging, odorless, mild; lamellae just free, rounded behind, ventricose, inserted, close, medium broad, fimbriate, white, unchanging; spores amyloid, oblong, smooth, about 10–11 × 3–4 μ; stipe slightly tapering downward to bulb, white, unchanging, glabrous at the apex with faint lines running down from the gills, floccose below the ring, about 8 × 1–1.3 cm.; rooting base 2.5 × 1.5 cm., volva limb white, flaring, about 1.5 cm. high and 2 cm. broad; annulus large, white, persistent, fixed 1 cm. from apex.

Type collected by W. A. Murrill under a laurel oak in Gainesville, Fla., June 28, 1944 (*F 38906*). Remarkable for its pearly appearance when dry. Rare.

Venenarius tenuifolius sp. nov.

Pileo conico-expanso, gregario, 6–8 cm., subviscido, glabro; lamellis adnatis, confertis, albis, fimbriatis; sporis cylindricis, 12 × 5 μ; stipite bulboso, albo, 7 × 0.7–1.3 cm.; volva vaginata; annulo parvo, albo.

Pileus conic to expanded, gregarious, 6–8 cm. broad; surface slightly viscid, smooth, glabrous, shining when dry, white, becoming yellowish on the disk with age or on drying, margin even, entire; context thin, fragile, white, unchanging, odorless; lamellae adnate, close, narrow, thin, much shriveled on drying, white, unchanging, fimbriate; spores cylindric, smooth, about $12 \times 5\ \mu$; stipe enlarged downward to the large bulb, white, unchanging, pruinose above, glabrous and shining below, about 7×0.7–1.3 cm., bulb 2.5 cm. thick; volva large, membranous, white, persistent, sheathing, with ragged margin; annulus small, white, fixed very near the apex of the stipe.

Type collected by W. A. Murrill in soil at the base of a laurel oak in Gainesville, Fla., June 22, 1944 (*F 38002*). Ten hymenophores were found growing in a very small area. They suggested *V. vernus* but the stems were too short. The cylindric spores, of course, distinguished them at once. In age or when drying there is a slight carrion odor. Rare.

For those using Saccardo the species described above are recombined as follows:

VENENARIUS MARGARITA = **Amanita margarita**
VENENARIUS TENUIFOLIUS = **Amanita tenuifolia**

W. A. MURRILL

PROF. V. A. TRANZSCHEL, 1868–1942

In the passing of Vladimir Andreevich (Woldemar Heinrich) Tranzschel on January 21, 1942 in besieged Leningrad science lost one of the oldest and most outstanding of Russian mycologists, a specialist of international standing on Uredineae.

Tranzschel was born on Jan. 4(16), 1868 in St. Petersburg and was educated at the University of the same city, where his teachers were such well known botanists as A. N. Beketov, C. Gobi, A. A. Famintzyn and I. P. Borodin. His strong inclination to botany urged him to join a small group of students, such as A. N. Krasnov, Robert von Regel, N. I. Kuznetsov, etc., who spent all their spare time in field botanical work and on heated discussion of taxonomic problems, and all of them were to become prominent scientists in the future. It was a good school for a young, energetic and hard

working student of natural history. He early became interested in cryptogams and his thesis work—*An enumeration of Uredineae of St. Petersburg Province* (Russian, 1888)—is an important contribution to that field of botany.

After his graduation in 1889 he became assistant in cryptogamic botany and curator of the Botanical Museum of the St. Petersburg University but the next year he went to St. Petersburg Institute of Forestry as an assistant of Prof. Borodin. Here he had an opportunity to study the rich mycological flora of the famous park of the Institute. In 1897 he worked for some time in the laboratory of the Biological Station at Bologoe and published a long enumeration of the fungi of the Valdai region (1901). From that time he started to pay more and more attention to biology and phylogeny of fungi. In 1898 he was transferred to the University of Warsaw as an assistant in plant morphology and systematics but in 1900 returned to St. Petersburg to become curator of the Botanical Museum of the Academy of Sciences. Since then, he was always connected with the Academy, becoming senior botanist of the Institute of Botany in 1912, the position he held until his death.

Tranzschel was an outstanding research worker, and a keen observer, who combined a perfect experimental technique with profound and cautious evaluation of experimental results.

His chief interest was in Uredineae to the study of which he devoted more than 50 years of his fruitful life. He was first to establish and prove experimentally the relationship between aecidial stages of rusts and their teleutospores on various host plants. It is known as "law or method of Tranzschel" and it is his most important contribution to the science of mycology. This problem is discussed in the two following works: *Ueber die Möglichkeit die Biologie wirtswechselnder Rostpilze auf Grund morphologischer Merkmale vorauszusehen* (1904) and more in detail in *La règle Fischer et la méthode Tranzschel" chez les Uredinées* (Russian, 1934).

Among his other works can be mentioned, as more important, *Contribution à l'étude du genre Triphragmium auct.* (1923) in which he divided this genus into three genera (*Triphragmium* Link, *Triphragmiopsis* Naum. and *Nyssopsora* Arth.) on the ground of

the affinity of host plants affected by these rusts. His interest in the phylogeny and evolution of fungi found expression in two important works—*Die Rostpilze in ihrer Beziehung zur Systematik der Gefässpflanzen* (1927) and *Les Uredinées comme indicateurs de l'affinité de leur hôtes en rapport avec l'évolution phylogénétique de ces champignons* (Russian, 1936). The results of his fifty years' study of rusts of Russia are incorporated in one of his last and most important works—*Rusts of the USSR* (Russian, 1939) in which he described 844 species of rusts occurring in the USSR and 288 species which possibly exist in that country. The parasites of each family are segregated into natural groups.

When Tranzschel came to the Botanical Museum of the Academy, the cryptogamic herbarium was practically non-existent. Now it may be considered one of the best in Europe. But it would be a great mistake to consider Tranzschel as a mere herbarium botanist. He was too active for such a role. He was an ardent traveller and collector. As a young man he collected in Vyborg (Vipuri), Novgorod and St. Petersburg provinces. In 1899 he visited Germany, Austria and Switzerland and in 1903 again was in Germany and in Switzerland, where he studied the mycological flora of the Swiss Alps. His trips in Russia were so numerous that we can mention only the most important ones. He explored Kirghizistan in 1900 and collected in Alai and Transalai Mts. (Turkestan). He made two trips to Ussuri and Primorsk regions in 1927 and 1929, the result of which he presented in two papers—*Uredinalium species novae ex Sibiria* (1933) *and Zur Biologie der Uredineen des Fernen Ostens* (1940). He also collected for a number of years in the Crimea.

He always identified his own collections as well as those of his numerous correspondents. He also cultivated an exchange of specimens with European and American mycologists. All this material of great scientific value is deposited mostly in the Cryptogamic Herbarium of the Institute of Botany at Leningrad.

Besides this, he took a very active part in editing with A. A. Jaczewski and V. L. Komarov, *Fungi Rossiae exsiccati,* 7 fasc. (1895–1900), and started in 1910 in collaboration with V. A. Serebriannikov another publication of a similar kind under the title *Mycotheca rossica,* 7 fasc., which existed until 1912.

Although of ripe age, Tranzschel was very active; besides his routine work, he lectured in many educational institutions, was a prolific writer and always took part in all scientific meetings and conferences. The strain of terrible sufferings in besieged Leningrad broke his health and added the name of this distinguished scientist, whose work was not only of great theoretical value but of immense practical importance to his native country, to the long list of victims of total war.

The sources consulted: A. S. Bondartsev, *The seventieth anniversary of birth of Prof. V. A. Tranzschel,* etc. in Priroda (1938) (4): 147–153, and R. Singer in Science **99**: 443. 1944.—VLADIMIR C. ASMOUS.

MYCOLOGIA

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ARTHUR HENRY REGINALD BULLER

FRED J. SEAVER

(WITH PORTRAIT)

In the death of A. H. Reginald Buller the Mycological Society of America has lost a charter member, a life member, and a loyal supporter. His loss will be felt not only by the Society, but by mycologists throughout the world. His life was so full that it would be impossible in the space available to even begin to enumerate his activities and list his publications. Perhaps it will serve our purpose to quote a brief biography prepared by one of his colleagues, G. R. Bisby, for Nature (**154**: 173. 1944):

"Arthur Henry Reginald Buller was born in Birmingham on August 19, 1874. His biological training included work at Mason College, Birmingham, at Leipzig, Munich, and (in 1900) at the Marine Biological Station, Naples. He then returned to Birmingham as lecturer in botany until, in 1904, he was appointed first professor of botany in the University of Manitoba.

"The young and booming city of Winnipeg delighted Prof. Buller, and the cold, bracing winters suited him. He entered with enthusiasm and energy upon his teaching, which at first included geology as well as botany. He prepared all his lectures and laboratory courses with great care, and transmitted something of his scientific spirit to his students. He did much, with the few other faculty members, to promote the growth of the young University.

[MYCOLOGIA for March–April (37: 163–274) was issued April 6, 1945.]

"At night during the long winters, and in any free time by day, he devoted himself to researches on the fungi. With painstaking, persistent care, and with much ingenuity in the use of simple apparatus, he sought out the details of such activities as the production, liberation, and dispersion of spores in *Coprinus* and other fungi. Few could lose themselves so completely in their work as he; but, since he never married and always lived at a hotel, the missing of a meal or a night's sleep disturbed no one.

"One of the attractions of the position at Manitoba was the long summer holiday which allowed him to spend three or four months each year at Birmingham, where he worked in the laboratories or library, or studied Nature in the woods and fields, commonly with his friend W. B. Grove. In later years he spent much of each holiday at Kew.

"Although Buller had published several papers in scientific journals, by 1909 he had enough material for a book to be entitled 'Researches on Fungi.' He submitted his manuscript to a society, but was told it could not be published unless it were reduced by about half. That, he considered, would be mutilation. He therefore published the book at his own expense—and later five more volumes even larger. Many mycologists and others have found this *magnum opus* not only of great scientific value, but also eminently readable. Other books included 'Essays on Wheat' and a 'Practical Botany' for students.

"On returning to Winnipeg each year about the end of September, he started his classes and then took advantage of the usually glorious Canadian autumns for a few mycological forays. Alone or with students, and later with members of the mycological colony which gathered at Winnipeg, he went for one or a few days into the primeval woods at Kenora or Minaki. He was a most stimulating leader of such excursions, for he knew not only the names but also the habits of the larger fungi and was always ready to spend an hour or two, even in heavy rain, to discover any new detail.

"Professor Buller gradually built up a strong department of botany and, though there was no graduate school for several years, he helped train a number of mycologists and other men of science

now prominent in Canada. He took great interest in the Dominion Laboratory of Plant Pathology, which began at Winnipeg in 1923. He was always ready to help any co-worker.

"Many honours came to him, including the presidency of the British Mycological Society, of the Botanical Society of America, and of the Royal Society of Canada. He was awarded the LL.D. by the Universities of Manitoba and of Saskatchewan, and a D.Sc. by Pennsylvania. He was elected a fellow of the Royal Society in 1929, and awarded a Royal Medal in 1937. His popularity as a lecturer increased through the years, and he was frequently chosen to give important lectures or lecture courses in Canada and the United States.

"Buller's interests were broad. He knew by sight most of the flowering plants of England and of Manitoba, and many of the birds. He read much, and had memorized long passages from Milton and Shakespeare. He amused himself by writing verse (some of his limericks have international fame), by playing the piano, by conversation—preferably regarding fungi, but with interest on any subject. He listed his recreations as 'billiards and crossing the Atlantic' and, though he found little time for the former, he made about sixty-five trans-Atlantic journeys (surely a record for a botanist). He had assumed, when he became professor emeritus at Manitoba in 1936, that his Atlantic crossings would end on an even number. However, the outbreak of war caught him at a congress in New York, so he returned to his researches at Winnipeg, varied with a number of lecture trips. In Winnipeg—which, after all, had been his main home for forty years—he developed a tumour on the brain which entailed weeks of hopeless struggle, and caused him worry because all his planned researches were not completed. He died on July 3, 1944, and is survived by a sister in London."

G. R. BISBY

TWO NEW SPECIES OF THE TILLETIACEAE FROM ARGENTINA [1]

Elisa Hirschhorn [2]

(with 3 figures)

Tilletia Phalaridis sp. nov.

Soriis in ovariis, 2–2.5 mm. longis × 1 mm. latis. Spores atratis flavescentibus, globosis, subglobosis vel irregularibus, 24.5–26μ diam.; episporis tuberculato, tuberculis irregularibus et conicis et echinulatis; membrana hyalina vestitis.

Hab. *Phalaris angusta* Nees. Rep. Argentina, Santa Fe, Instituto de Investigaciones Agricolas, leg. *P. R. Marco,* in herb. *L. R. Parodi* No. *14737,* type in herb. E. Hirschhorn No. *2005.*

Attacking the inflorescence and developing at the expense of the ovaries, leaving the remainder of the plant intact. Sori sand-colored, oval, 1 × 2–2.5 mm., fragile, covered by a cinnamon-colored membrane, prolonged at the apex to form a little apiculum. Chlamydospores pale yellow, globose, sub-globose, or irregular, 24.5–26 μ in diameter; epispore very coarsely tuberculate, the tubercles irregularly conical, finely echinulate, concave at the apex, 3–4 × 3.5–11 μ high; enveloped in a thin hyaline membrane which exceeds the diameter of the chlamydospore (fig. 1, A and B). Sterile cells hyaline or slightly yellowish, oval or globose 14 × 17–18 μ; epispore 3–3.5 μ thick, finely echinulate (fig. 1, C and D).

Obs. I. The glumes almost entirely cover the sorus, which makes detection of the parasite difficult.

I have not been able to observe germination, even after many attempts with different treatments and different media.

[1] Published as Scientific Paper No. 605, College of Agriculture and Agricultural Experiment Stations, State College of Washington, Pullman, Washington.

[2] Assistant in Plant Pathology, State College of Washington, Pullman, Washington. Grateful acknowledgment is made to George W. Fisher for assistance in the preparation of the photography.

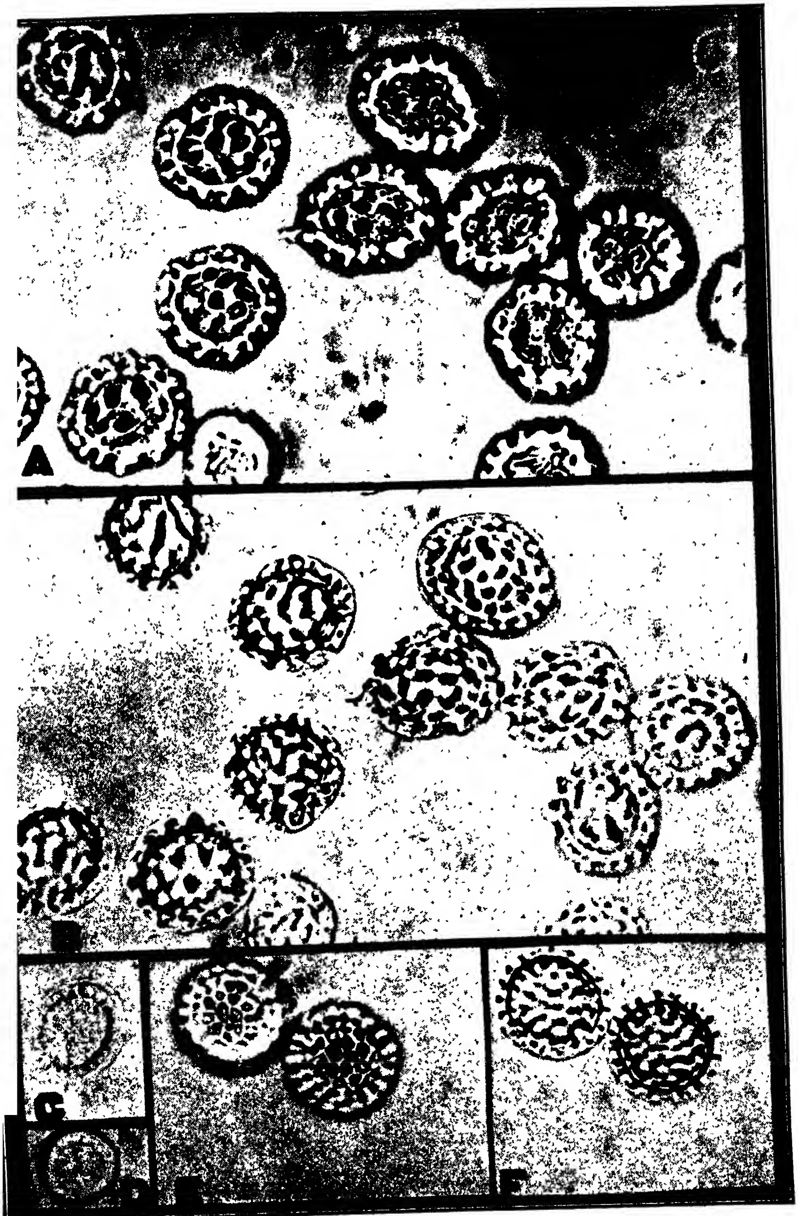

FIG. 1. A–D, *Tilletia Phalaridis*. A, photomicrograph of the chlamydospores, surface view; B, *ibid.*, same group of spores, median view; C and D, sterile cells; E, *Tilletia Menieri*, surface view; F, *ibid.*, same spores, in median view.

Obs. II. On *Phalaris colorata* (= *P. arundinacea* L.), in France, Harriot and Patouillard [3] described *Tilletia Menieri.* Study of the type material of this species [4] has proven it to be distinct from *T. Phalaridis.* The spores of *T. Menieri* are definitely reticulate and are not enveloped in a hyaline membrane (FIG. 1, E and F), as compared with *T. Phalaridis,* the spores of which are tuberculate and enveloped in a hyaline membrane (FIG. 1, A and B).

Glomosporium Amaranthi sp. nov.

Soris in ovariis, colore cinnamommis, globosis, 1–1.5 mm. diam, compactis glomerulis auratis fuscis, globosis vel irregularibus, 60–89μ diam., vel 70–143 × 65–93 μ diam. Sporis colore cinnamommis vel auratis transparentibus, 12–17μ diam. vel 12 × 20μ diam.; episporis verrucoso.

Hab. *Amaranthus* sp. Argentina: Salta, Oran. leg. *Hunziker,* No. *2309.*

Attacking the inflorescence and developing at the expense of the ovaries. Sori 1–1.5 mm. in diameter, globose, cinnamon-colored, slightly compact and granular; enveloped in a thin membrane (probably the epidermis of the ovary). Spore balls dark golden or very slightly orange, globose, 60–89 μ in diameter or irregularly elongated, 65–93 × 70–143 μ.

Chlamydospores cinnamon-yellow, polygonal, 12–17 μ in diameter, or 12 × 20 μ; epispore thin, densely and prominently verrucose.

Obs. I. Paraffin sections of the sori and spore balls of *Glomosporium Amaranthi* have been studied. Figure 3 shows the appearance of the sorus in cross section. It is composed of the wall, which appears to be parasitized host tissue and almost a

[3] Harriot, P. and Patouillard, N. Description de Champignous nouveaux de l'Herbier du Museum. Bull. Soc. Myc. France 20: 61–65. 1904.

[4] Vestergren, Mycromycetes rariores selecti No. 1067.

FIG. 2. *Glomosporium leptideum* and *G. Amaranthi.* A, *G. leptideum,* group of spore balls, surface view; C, *ibid.,* same group of spore balls, median view; B, *ibid.,* reproduction of original illustration, median view; E, cross section of spore balls of *G. Amaranthi,* to show internal structure; F, spore balls of *G. Amaranthi,* surface view, same two spore balls as in lower right in D.

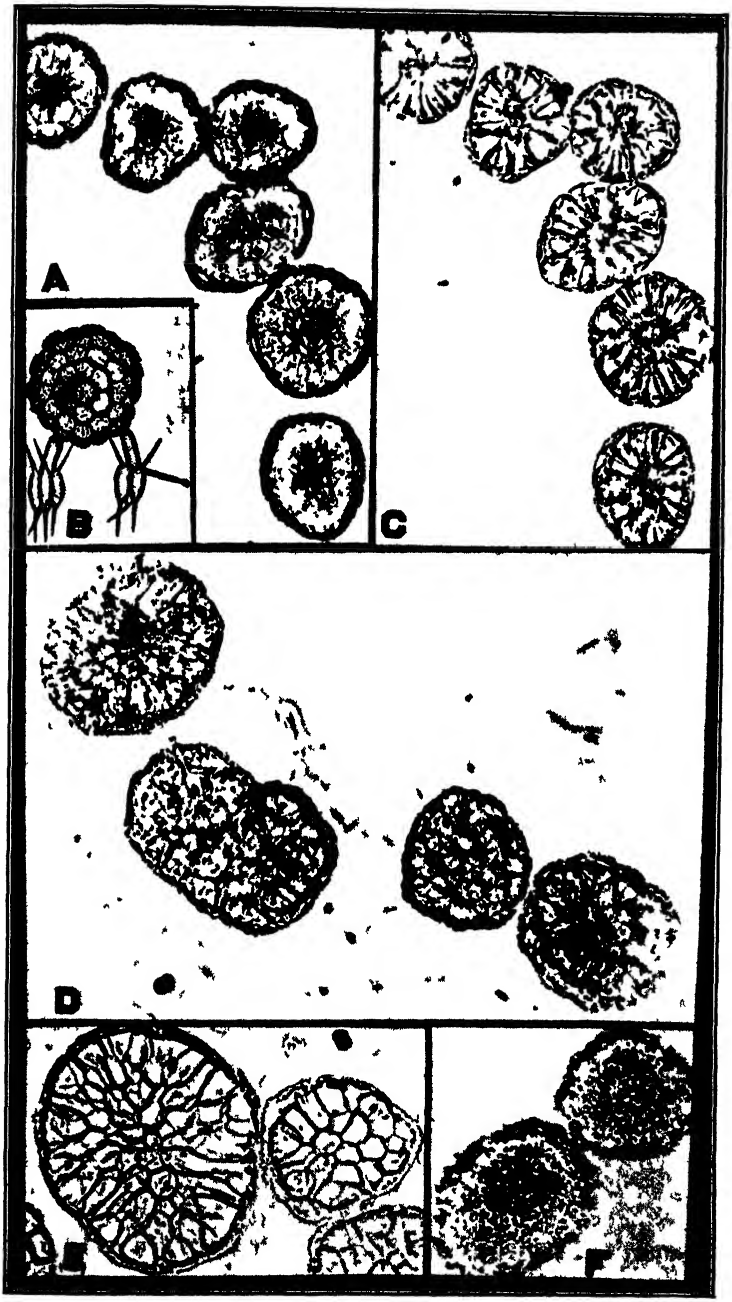

FIG. 2

solid mass of spore balls. The spore balls themselves are solid in structure, and apparently are composed solely of spores, without central or peripheral cortex (FIG. 2, E).

Obs. II. Not all of the ovaries are attacked by the fungus, and the ones escaping produce apparently normal seeds.

The sori are so small and inconspicuous that they are difficult to detect.

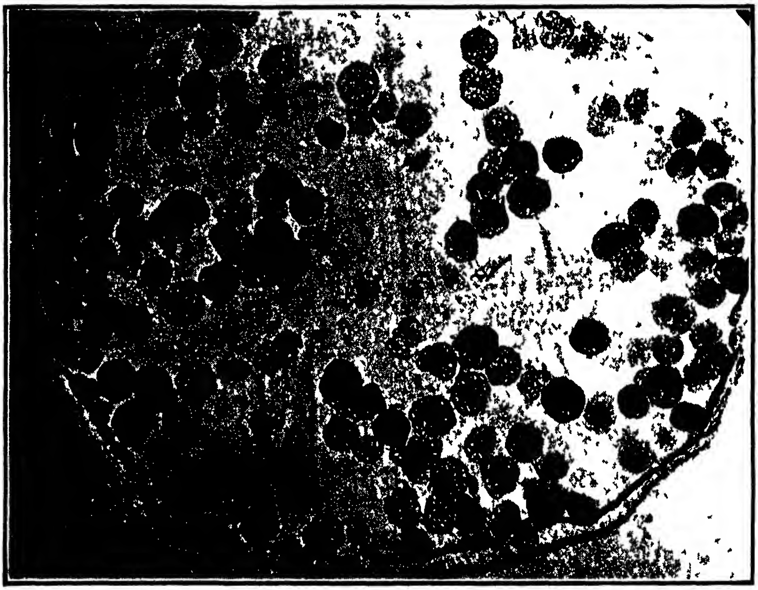

FIG. 3 *Glomosporium Amaranthi*, cross section of the sorus, to show structure and disposition of spore balls

Obs. III. The genus *Glomosporium* was described by *Kochman,* according to *Zundel,*[5] in 1939, based on *Tolyposporium leptideum* Sydow which attacks *Chenopodium album* in Europe. The basis of *Kochman's* new genus of the Tilletiaceae is the character of the promycelium, which was found to bear a terminal cluster of 3–4 sporidia (FIG. 2, B).

Glomosporium Amaranthi differs from *G. leptideum* by its larger, darker, and more irregular spore balls, and by the more pronounced verruculations of the epispore (FIG. 2, A, C, D, F).

[5] Zundel, George L. Notes on the Ustilaginales of the world III. Mycologia 35: 164–184. 1943.

Until now, *Glomosporium* has been considered a mono-typic genus, with *G. leptideum* as the only species. A careful comparison of the smut on *Amaranthus* with type material [6] of *G. leptideum* leaves no doubt that two different entities are concerned. I have not been able to observe germination of the smut on *Amaranthus,* and for this reason it is provisionally assigned as a species of *Glomosporium.* The permanent smut balls also suggest the genus *Tolyposporium.* However, this genus is characterized by the spores being bound together by thickenings of their outer walls, to which character the smut on *Amaranthus* does not conform.

EXSICATTI EXAMINED: Germany: Forbach Lotharingiae, 9, 1913. Leg. A. Ludwig. Sydow *Ustilagineen* No. 475 (Typus of *Tolyposporium leptideum* Sydow) on *Chenopodium album* L.: Nahrpflanze, 27–8–14, Flora von Forbach in Lothringen, Herbarium A. Ludwig, on *C. album: ibid.,* 9–1913, leg. Dr. A. Ludwig. Dr. Zilligs *Ustilagineen* Herbarium, Typus of *Tecaphora leptideum* (Syd.) Zundel, on *C. album;* New South Wales Department of Agriculture, Biological branch, 1941, N. S. W., on *C. ambrosioides;* Moravia, 1–9–23, leg. Ed. Bandip, on *C. album.*

STATE COLLEGE OF WASHINGTON,
PULLMAN, WASHINGTON

[6] Kindly supplied by Dr. G. L. Zundel.

SPECIES OF SYNCHYTRIUM IN LOUISIANA

I. DESCRIPTIONS OF SPECIES FOUND IN THE VICINITY OF BATON ROUGE

Melville T. Cook

(with 4 figures)

Synchytrium [1] is a genus of parasitic fungi belonging in the order Chytridiales and family Synchytriaceae. The individual fungus in all species consists of a single cell which lives the greater part of its life in an epidermal cell of a higher plant and in most species causes the formation of a gall or tumor. In the species reported in this paper the infections originate in the epidermal cells. These infected cells increase in size and either become surrounded by host cells which form the galls or become embedded as a result of the growth of the surrounding tissues.

The literature indicates that the species in the north temperate zone appear in the cool wet months of the spring and usually become less abundant during the warm months of summer. The Louisiana species described in this paper appear during the cool wet months of fall and disappear during the warm months of spring and summer.

After infection the host cell enlarges and the fungus grows and develops a thick wall which in some species is composed of three layers. When the fungus has attained its full growth it undergoes segmentation by the formation of membranes, which arise at the periphery, extend inward and finally form the sporangia. Zoospores are formed in the sporangia, escape and infect the young

[1] This genus was established by DeBary and Woronin. The name is a combination of the Greek *Syn* meaning *with* or *together* an *chytron* meaning a chamber. Ber. Nat. Ges. Freiberg **3**: 22. 1863. Synonyms—*Chrysophlyctis* Schilbersky, Ber. Deut. Bot. Ges. **14**: 36. 1896. *Pycnochytrium* (DeBary) Schroeter, Engler and Prantl, Nat. Pfl. I. **1**: 73. 1897. *Woroninella* Raciborski. Zeitschr. Pflanz. **8**: 195. 1898. *Miyabella* Ito & Homma. Mag. Tokyo Bot. Soc. **40**: 110. 1926.

epidermal cells of other plants. In some species several generations are produced in a growing season. All species appear to have a dormant stage which carries them over until next growing season. All the species described in this paper appear to produce several generations during the cool, wet months of winter, but some appear to produce more generations than others. All these species disappear during the warm months of summer. The colors of the fungi and the surrounding host plant tissues are quite different. The color of the fungus is pale lemon when young but becomes yellow or orange with age. The color of the gall is due to the color in the host cells and not to the color of the fungus.

Tobler recognized 63 species of *Synchytrium* and reports a few others that are less well known. The literature indicates 90 or more and in all probability there are many that have not been described. Most species have been reported on a single host, but a few have been reported on two or more host species. They have been reported from the temperate and tropical zones, mostly from the north temperate zone. Many of these organisms are injurious to their host plants, especially to seedlings. Sometimes young plants are killed or are injured so severely that there is little later growth. The life histories of most species are not well known and in many cases descriptions are not satisfactory. All species described in this paper, with the possible exception of the one attacking *Lepidium*, cause dwarfing, and the one on *Geranium* causes very pronounced malformations.

Species reported on the same host but from different parts of the world are not necessarily identical, although they have been considered the same by some authors. Herbarium material is not satisfactory for writing descriptions or making comparisons. Some of the herbarium specimens have been found to contain rusts which have undoubtedly been mistaken for species of *Synchytrium*. Some of the early descriptions appear to be incorrect.

Most species cause enlargements of the infected and surrounding cells and cause the formation of tumors or galls. Kusano has reported that *S. fulgens* causes very slight enlargements of the cells of *Oenothera*. In Louisiana the species attacking *O. laciniata* and supposed to be *S. fulgens* causes pronounced enlargements

of the infected cells and thickenings of the leaves, due to an increase in the amount of mesophyll. It is possible that the Louisiana species on *O. laciniata* may be different from the one studied by Kusano on *O. biennis*. All other species studied by the writer cause very definite galls which are characteristic of the species and very important in writing descriptions and making determinations.

The descriptions in this paper are based on fresh material and the arrangement is based on the structure of the gall beginning with the simplest. The life histories of the fungi are so similar that the characters of the galls appear to be more reliable for determination of the species than the characters of the fungi. Even the measurements of the fungi are so variable as to be unsatisfactory for diagnosis, and the number of sporangia in a sorus is extremely variable. All species may cause simple or compound galls but compound galls are least common in *S. Hydrocotyles*. These compound galls may be due to crowding of infected cells or to the infection of the epidermal cells of a gall. The infection of a host cell by two or more zoospores is quite common, especially in *S. Chiltonii* on *Stellaria media*.

The descriptions of six new species and two which have been previously described are included in this paper.

SYNCHYTRIUM FULGENS Schroeter 1873.

Infections numerous on both surfaces of leaves and projecting slightly; on petioles and stems, simple or compound, not completely closed by growth of host cell; red, orange, or black; 88–116 μ in diameter; malformations are most pronounced over veins; no true galls as in most species but leaves become thickened; leaves become yellowish or reddish; thicker than normal and slightly roughened due to slight projections of epidermal cells, reddish and projecting, over sori; the thickenings are more pronounced on lower (*i.e.* in the mesophyll) than on upper surfaces; sori not completely covered by epidermal cells but appear to be sunken in the tissues of the host plant; sorus completely fills host cell, 15 × 24 to 42 × 42 μ in diameter; sporangia polyhedral, becoming spherical, walls thick and hyaline; 3–5 μ in diameter.

Habitat: *Oenothera laciniata* Hill.

FIG. 1. A, *Synchytrium fulgens,* natural size; B, *S. modioliensis,* × 5½; C, *S. Chiltonii,* × 1½.

Synchytrium modioliensis sp. nov.

Galls on both surfaces of leaves, petioles, stems, and ovaries (seed pods); usually simple, spherical, sori completely closed over by the host tissues; very little modification of the leaf structures; palisade cells slightly depressed; leaves yellow in early part of season, red to black late in season; sori orange, becoming black, the host cells clear or red. Galls maximum 18 × 24 μ; fungus yellow to orange, 14 × 18 μ; sporangia 3½ × 7 μ.

Gallis sphaericis, numerosis in utraque superficie foliorum, petiolis stirpibusque; egregie simplicibus; superficie plantae contagiis (punctis) contactus cum gallis minute (leviter) depressa; gallis flavis, dein in colorem aurantiacum, rubrum aut nigrum se mutantibus; 18 × 24 diam.; soris aurantiacis, 14 × 18 u; sporangiis 3½ × 7 μ diam.

Hab. *Modiola caroliniana* (L.) G. Don.

Synchytrium Chiltonii sp. nov.

Galls numerous, submerged in both surfaces of thickened leaves, enlarged petioles, enlarged stems, parts of flower and in buds; galls usually simple, flask-shaped but not closed; the basal part embedded in the tissues of the host; infected parts light green or yellowish; larger galls 70 × 83 μ in diameter; plants dwarfed and stems swollen; sori 48 × 48 μ in diameter; sporangia 3½ μ or more in diameter.

Gallis numerosis in utraque superficie foliorum densatorum in petiolis amplificatis, in stirpibus auctis ampliatis et in partibus gemmarum florumque; egregie simplicibus ampulliformibus parte basali in hospitis textum submersa sed epidermide hauf clausa; 70 × 83 μ in diam.; plantis impeditis et partibus earum infectis tumidis; subviridibus aut subflavis; soris immersis, 58 × 58 μ diam.; sporangiis 3½ vel plus diam.

Hab. *Stellaria media* (L.) Cyrill.

Spegazzini (1881) described *S. australe* on *Modiola prostrata* in Argentina but the description is quite different from the above.

Fuckel (1869) described *S. Stellariae* on *Stellaria media* and *S. nemorum* in Germany but the description is quite different from the above.

Synchytrium Cerastii sp. nov.

Galls mostly submerged in tissues on under surface of leaves, petioles, and stems; not numerous until late in season and not

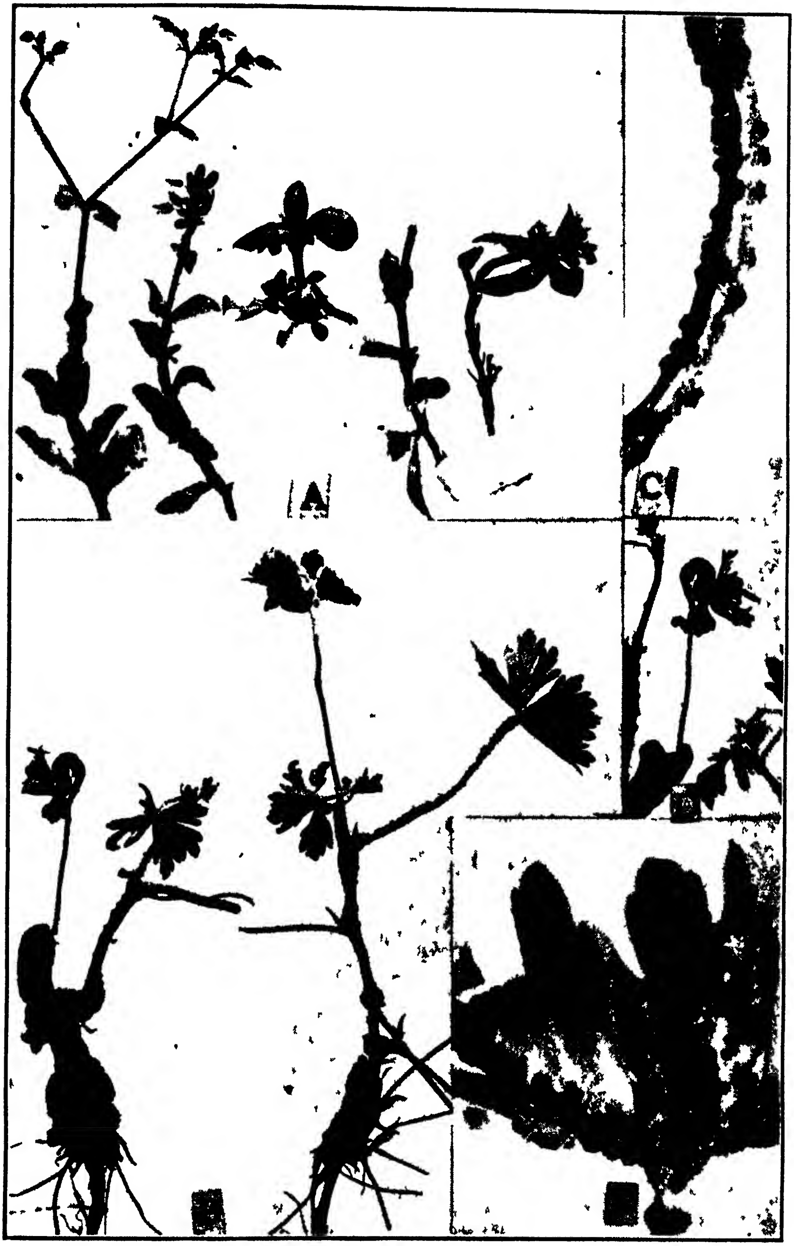

FIG. 2. A, *S. Cerastii*, slightly reduced; B–E, *S. Geranii*, B, slightly reduced; C, × 5½; D, slightly reduced; E, × 5½.

found in flowers; flask-shaped; green and difficult to see in early part of season; pale yellow and finally black in late part of season; maximum 56 × 63 μ in diameter; sori 28 × 28 μ in diameter.

Gallis maximam partem sub foliorum superficiebus in petiolis stirpibusque; haud numerosis ad anni tempus paene peractum; pallide flavis in colorem nigrum tempore anni fere peracto se mutantibus ampulliformibus, 56 × 63 μ diametro; soris immersis, epidermide haud clausis, 28 × 28 μ diam.; sporangiis paucis 3½ μ vel plus diametro.

Hab. *Cerastium viscosum* L.

The infections start later than those on *Stellaria media,* persist longer and are not so numerous but become quite abundant and conspicuous late in the season.

The flask-shaped inclosing cells are smaller than in *S. Chiltonii,* sporangia fewer, fungus more sensitive to stain.

SYNCHYTRIUM GERANII Clen.

Galls on all parts of the plant but rare in the bud and flower; very abundant on stems and leaves, most abundant on upper surface of leaves, red, simple or compound, not closed; lower half embedded in host tissue; sometimes the infections are so severe as to cause distortions of stems and leaves, stem sometimes much thicker than normal. Galls 130 × 130 μ in diameter, rarely larger; sori 73 × 73 μ in diameter; maximum size of sporangia 7½ μ in diameter.

Hab. *Geranium carolinianum* L.

Synchytrium Edgertonii sp. nov.

Galls occur on either surface of leaves and on petioles; small, white, becoming brown with white border and finally entirely brown and brittle; simple or compound, closed, project on either or both surfaces of leaves, becomes black with age. When mature the host tissues break down, leaving a hole in the leaf. Galls 63 × 63 to 14 × 140 μ in diameter; sori submerged, 82 × 82 μ in diameter; sporangia 4–7 μ in diameter.

Gallis in utraque superficie foliorum et petiolis, simplicibus aut compositis ex alterutra aut utraque superficie eminentibus, viridibus, in colorem nigrum aetate se mutantibus. Gallis maturis, 63 × 63 ad 140 × 14 μ diametro, textus hospitis se refrigit utque eo foramina in foliis relicta sunt soris immersis 82 × 82 μ diametro; sporangiis 4–7 μ diametro.

Hab. *Dichondra repens* Forst.

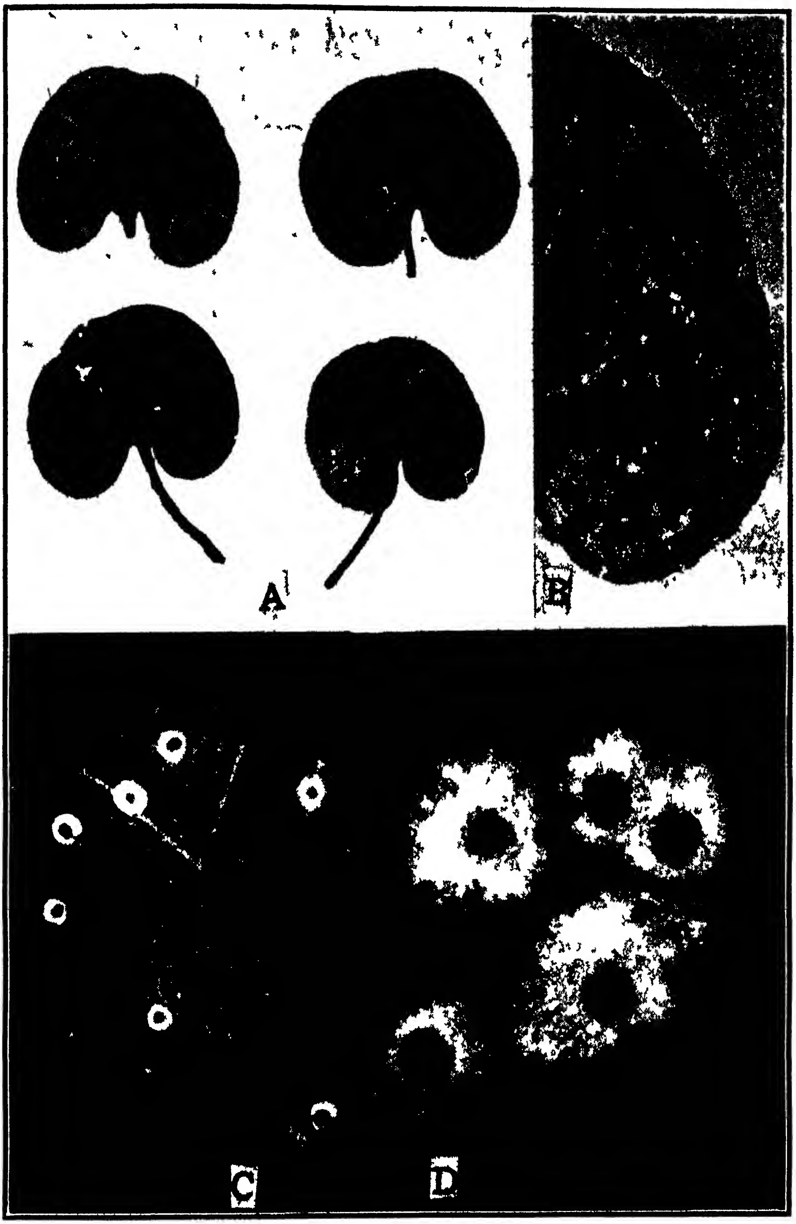

FIG 3. A–D, *S. Edgertonii*, A, × ½, B, × ½ from dried specimen, C, enlarged; D, enlarged.

FIG. 4 A–B, *S Lepidii*, A, natural size, B, × 5½, C, *S Hydrocotyles*, × ½

Synchytrium Lepidii sp. nov.

Galls on leaves (usually lower surface), petioles, and stems; very large, simple or compound, closed; sometimes projecting equally on both surfaces of leaves and sometimes resting on the surface of host plant. Early infections inconspicuous, green, becoming pale yellow and grayish or brown with age. Galls 130 × 130 to 175 × 175 μ in diameter; sori 40 × 40 to 52 × 52 μ in diameter; sporangia about 4 μ in diameter.

Gallis in foliis, petiolis stirpibusque, in alterutra superficie foliorum aut ex alterutra aut utraque eminentibus; simplicibus vel compositi; manifestis viridibus, pallide flavis subgriseis in colorem brunneum aetate se mutantibus, 130 × 150 ad 175 × 175 μ diametro; soris 40 × 50 ad 52 × 53 μ diametro; sporangiis 4 μ diam.

Hab. *Lepidium virginicum* L.

Synchytrium Hydrocotyles sp. nov.

Galls mostly on the under surface, usually causing a pit on the under surface and a dome on the upper but the reverse may occur; black spot at bottom of pit indicates point of infection. Sometimes a papilla is formed at the bottom of the pit. Sometimes a papilla is formed on the margins of leaves without the pit. The dome may become pale yellow; the papilla may be darkened and the entire gall may become black, especially in the margins of the leaves. Fungus orange. Galls closed, maximum size 175 × 280 μ in diameter; sorus lemon yellow, becoming orange, 42 × 42 μ in diameter. Some on either side; black spot at bottom of dome indicates point of infection. Fungus lemon yellow becoming orange.

Gallis in foliis petiolisque; tholoideo cum papillis nigris in latere concavo puncto contagionis (contagi); tholo pallide lurido flavo; papillis rubidis vel nigris in-marginibus praecipue foliorum; gallis 140 × 175 ad 175 × 280 μ diametro; soris limono-flavis vel aurantiacis, 42 × 42 μ diam.

Hab. *Hydrocotyle umbellata* L. et *H. Canbyi* Coult. and Rose.

Spegazzini (1881) described *S. bonaerense* on *Hydrocotyle bonaerensis* in Argentina but the description differs from the above.

The writer wishes to thank Dr. C. W. Edgerton, Dr. Clair A. Brown, Dr. L. H. Flint, Dr. S. J. P. Chilton, and others who have assisted the writer in making these studies.

DEPARTMENT OF BOTANY,
LOUISIANA STATE UNIVERSITY,
BATON ROUGE, LA.

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SOME NOTEWORTHY RUSTS—I

M. J. Thirumalachar

(with 21 figures)

In the course of studies on the rust flora of Mysore State (South India) large collections of a rust on the leaves of *Ichnocarpus frutescens* Br. were secured from various localities. The rust had for the most part only uredial stages and completely agreed with the descriptions of *Uredo Ichnocarpi* Barclay. This was further confirmed by comparative studies with a specimen obtained from the Herb. Crypt. Ind. Orient. New Delhi. The uredia, which can be collected almost all the year round, are subepidermal (fig. 1), occurring in large numbers and completely covering the underside of the leaf. Many of the sori are also epiphyllous. The infection spots can be made out as pale yellow specks on the dark green surface of the leaves. The urediospores are golden yellow, developing singly on pedicels (fig. 1). The ruptured epidermis is very conspicuous and the sori are aparaphysate. The exospore is minutely and densely verruculose. The germ pores are indistinct and become visible only at the time of germination.

The urediospores readily germinate when placed on slides in a moist chamber. The tip of the germ tube becomes swollen developing an appressorium. Inoculation experiments revealed that the urediospores readily infect the same host, causing the formation of secondary uredia. A close watch was kept on all the infected plants to observe any telial stages for the rust, if present, which might enable one to establish the identity of the rust. It was, however, noticed that the rust could perenniate in most cases in the uredial stage itself, as in the cases of some tropical rusts. But the formation of telia was noticed developing both within the uredia as well as separately. This afforded an opportunity to study the rust in some detail.

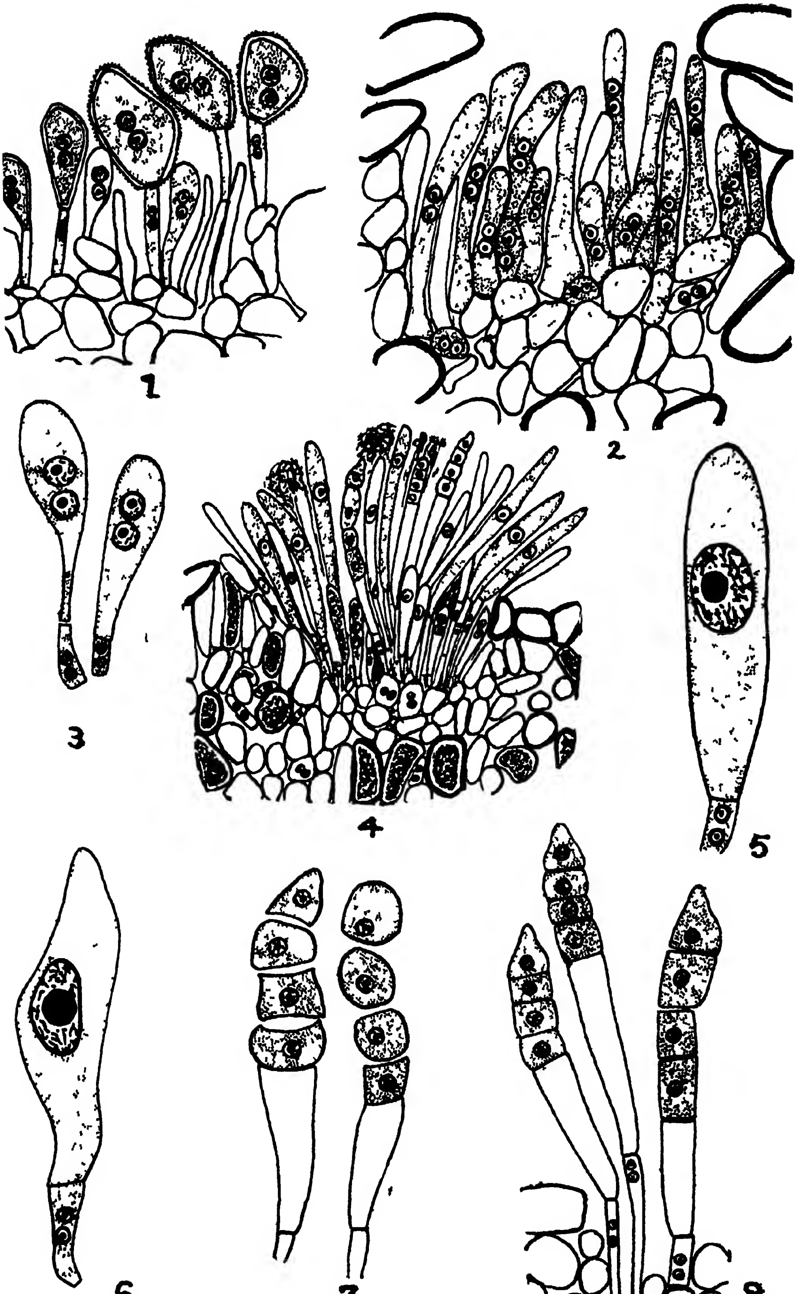
The material for microscopic studies was fixed in Allen's modification of Bouin's fluid and stained with Heidenhain's iron-alum

haematoxylin, with eosin-B in clove oil as counterstain. The development of the spore forms and all the morphological details were studied in microtome sections. The urediospores are golden yellow, developing singly on pedicels and agreeing in all respects with *Uredo Ichnocarpi* Barclay. Sydow and Petrak (**1928**), who founded the genus *Achrotelium* on *Ichnocarpus Volublis* from the Philippines, state that *Uredo Ichnocarpi* found in India might also belong to the same rust genus *Achrotelium.*

The telial stages of the rust which have been recorded in the present study clearly indicated that the rust is not cogeneric with *Achrotelium.* The telia appear as fluffy pustules and easily can be mistaken for old uredia. The teliospores have been found developing within the uredia, thus indicating the genetic relationship between the two spore forms. The telial initials are subepidermal in origin (FIG. 2). Small hyphoid cylindric cells borne on short pedicels mark out young telia (FIG. 3). As development proceeds, the sorus becomes organized, consisting of long clavate, hyaline teliospores borne on short pedicels. The shape of the sori, unlike as in other rusts, is like an acervulus (FIGS. 4 and 20). In the young teliospores the binucleate condition is conspicuous (FIG. 3) and a fusion nucleus is formed in the mature spores (FIGS. 5 and 6). The nuclei of the pedicels are also conspicuous surrounded by densely staining cytoplasm.

The teliospores germinate intrasorum soon after maturity (FIG. 7). Prior to germination the fusion nucleus in the teliospore slightly migrates upwards accompanied by the prolongation of the spore apex. The prolongation of the spore apex does not take place to appreciable extent so as to form a recurved promycelium as in rusts like *Maravalia* or *Scopella.* The distinction between the promycelium and the teliospore is lost soon after germination as they become uniformly broad throughout the length. The germinated spores can be differentiated from the non-germinated spores by being longer and narrower. The first wall is laid right

FIG. 1, uredium of *Acervulopsora Ichnocarpi*, × 640; 2, young telium, × 640; 3, young teliospore, × 800; 4, mature telium showing the acervulus-like sori, × 400; 5 and 6, mature teliospores, × 800; 7 and 8, germination stages showing the rounding off of the promycelial cells as basidiospores, × 800.



FIGS. 1–8.

in the center with the result that the promycelium thus separated includes the apical portion of the teliospore, and must be considered as being semi-internal.

Following the usual mode of development the promycelium becomes four-celled, each cell showing a conspicuous nucleus (FIGS. 8 and 21). The cells are very fragile and even in the early stages of development show a tendency to get separated. In later stages these cells get separated as round cells (FIGS. 7 and 21) which might directly function as basidiospores or develop secondary basidiospores, a feature not confirmed in the present investigation. The development of sterigmata with basidiospores at their tips has not so far been observed.

Following teliospore germination and the consequent rounding off of the cells of the promycelium into basidiospores, the pedicel also shows some amount of elongation. The germinated spores are pushed farther upwards than the rest of the ungerminated spores within the sorus. The pedicels which in the mature spores measure up to 13.5 μ elongate up to 48 μ in the course of the teliospore germination. After the dispersal of the basidiospores the portion of the teliospore beneath the promycelium collapses and gelatinizes. The pedicels remain persistent for a long time and can be observed as fusiform structures.

The structure and germination of the teliospore presents an interesting problem in the identity of the rust. That it is not *Achrotelium* is evident by the differences in the structure and germination of the teliospores. In *Achrotelium Ichnocarpi* Syd. Arthur and Cummins (**1936**) have shown that the teliospores arise in clusters on sporogenous basal cells and that the promycelium is internal, developing basidiospores on short sterigmata. This feature has been confirmed by Cummins (**1940**) in *A. Lucumae* Cumm. The teliospores of the rust under study on the other hand develop singly on pedicels and not in clusters and the basidium is semi-internal since there is a definite prolongation of the spore apex in the process of germination. In the genera *Chrysella* Syd. and *Goplana* Racib., the internal basidium is a distinguishing character, and particularly in the latter genus there is a gelatinous matrix embedding the teliospores.

The genera like *Maravalia* Arth., *Scopella* Mains and others can be distinguished from the present rust by the nature of the promycelium which is external and distinct from the teliospore. A wall separating the apex of the teliospore from the promycelium is considered to be an important character of the genus *Blastospora* Diet. Indeed, in the present rust the first wall is laid down lower still, following germination, including the apical half of the teliospore to the extent of its being semi-internal. Further, the superstomal telia present in *Blastospora* separates the two genera. Semi-internal promycelium is at present known only in two genera of rusts, viz. *Cystospora* Butler and *Zaghouania* Pat. which, however, possess other distinguishing characters.

In the possession of an acervulus-like telium and a fragile four-celled promycelium, the present rust shows a good deal of resemblance to *Chrysocelis* Lagerh. In *Chrysocelis Muehlenbeckiae* Lagerh. & Diet., for instance, Dietel (**1914**) reports that the telia are acervular, the basidiospores being formed by the rounding up of the cells of the promycelium (Dietel, **1928**). This situation reminds us of the condition present in the rust under study, but the semi-internal promycelia and stipitate teliospores are distinguishing features. The tendency of the pedicel to elongate following germination is also noticed in the case of *Chrysocelis ascotela* (Syd.) Thirumalachar (**1942**). While in these above mentioned characters there is a close resemblance between *Chrysocelis* and the present rust, the type of germination is a distinguishing character. For instance the genus *Chardoniella* is separated from *Chrysopsora* only by the internal basidium present in the latter. It is not always possible to seek evidences of spore germinations in identifying the rust genera, but when such evidences become available, they must be taken into account as they are critical stages in the life-cycle of the rusts. It is manifest that the present rust cannot be accommodated in any of the genera of rusts so far described and hence it is placed in a separate genus for which the following name is proposed.

Acervulopsora gen. nov.

Pycnia atque aecia ignota. Uredia subepidermalia; urediosporae singulis pediculis isidentes. Telia subepidermalia, erumpentia, acervulo similia, telio-

sporae clavatae, hyalinae tenuibus parietibus ornatae, singulis pediculis insidentes, maturae sporae germinantes in soro, producto sporarum apice; promycelium semi-internum (inclusa superiore parte teliosporae), 4-cellulatum; sporidia formantur rotundatis promycelii cellulis.

Species typica: *Acervulopsora Ichnocarpi* (Barclay) Thirumalachar.

Pycnia and aecia unknown. Uredia subepidermal, urediospores borne singly on pedicels. Telia subepidermal erumpent, acervulus-like; teliospores clavate, hyaline, thin-walled, borne singly on pedicels; germinating intrasorum at maturity by the prolongation of the spore apex; promycelium semi-internal (including the upper portion of the teliospore), four-celled; sporidia formed by the rounding off of the promycelial cells.

Type species, *Acervulopsora Ichnocarpi* (Barclay) Thirumalachar.

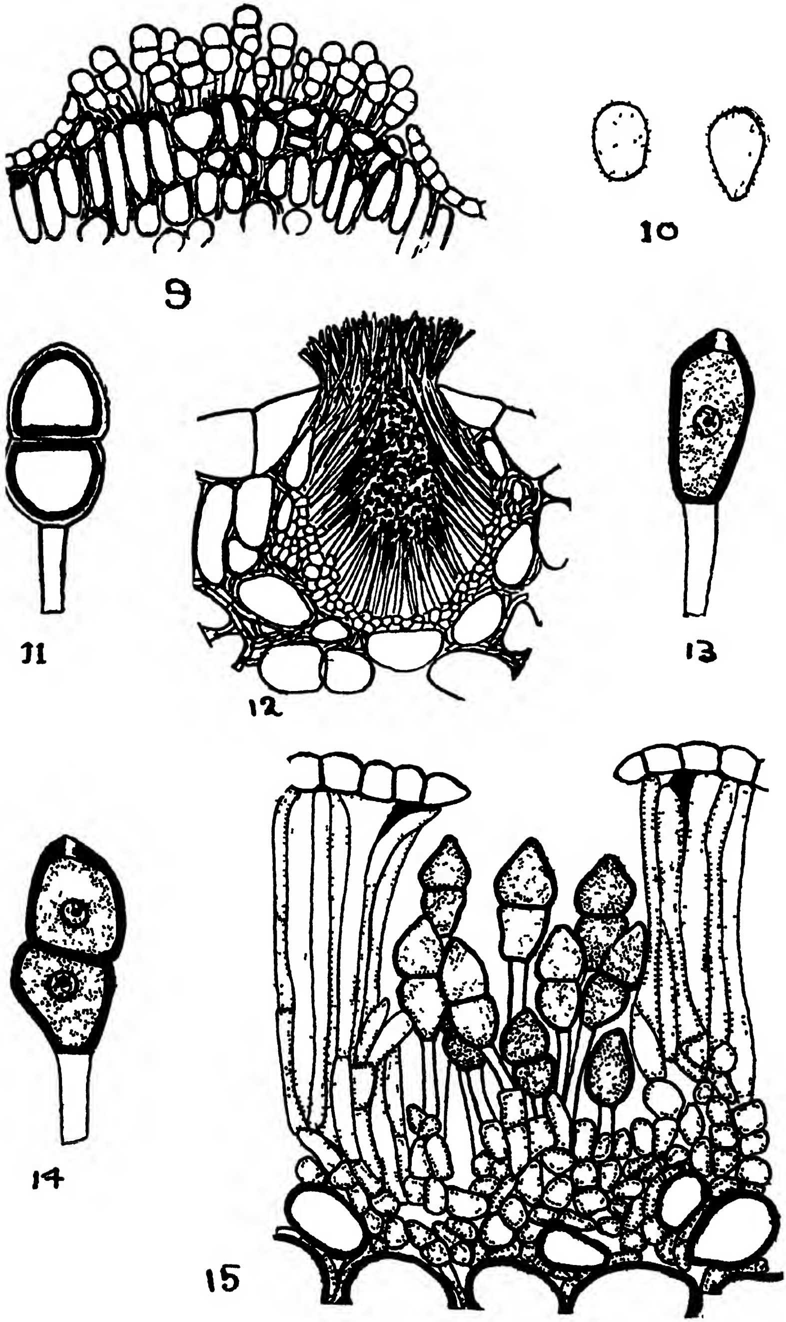
Acervulopsora Ichnocarpi (Barclay) Thirumalachar, comb. nov.

Uredia ut plurimum hypophylla, raro amphigena, subepidermalia, erumpentia atque aparaphysata; infectionis maculis pallide lutea, sorus flavidus; urediosporae obovatae vel ellipsoidae, minutae atque dense verruculosae, magnitudinis 19–25 × 15–20 μ germinationis poro indistincto, singulis pediculis insidentes. Telia primo in urediis, evolventia, deinde separate evoluta, albida atque languinosa, subepidermalia, acervulo similia, erumpentia; teliosporae clavatae, in utrinque apice rotundatae, magnitudinis 30–41 × 7–8.5 μ; pedicellatae; maturae sporae germinantes in soro, producto sporarum apice; promycelium semi-internum, primo pariete efformato in media teliosporarum parte; 4-cellulatum, sporidia producta rotundatis promycelii cellulis, fragilia, facile disjuncta, magnit. 5–8.5 × 7–8 μ. Pediculi hyalini, persistentes, crescentes ad 48 μ impellentes teliosporas germinantes supra ingerminatarum sporarum planum.

Habitat in foliis *Ichnocarpi frutescentes*, Yashavantapus (Mysore), 14–8–1942, leg. M. J. Thirumalachar (typus). Typus positus in auctoris herbario; in Herb. Crypt. Ind. Orient in Imp. Agric. Res. Inst. New Delhi; in Arthur Herbario, Purdue Univers. Lafayette, Indiana, U. S. A., in Herb. Imp. Mycolog. Inst. Kew. in Anglia.

Uredia mostly hypophyllous, rarely amphigenous, subepidermal, erumpent and aparaphysate; infection spot pale yellow, sorus golden yellow, urediospores obovate to ellipsoid, minutely and densely verruculose, measuring 19–25 × 15–20 μ with indistinct

FIG. 9, telium of *Puccinia Volutarellae*, × 400; 10, urediospores of *Puccinia bellurensis*, × 450; 11, teliospores of *P. bellurensis*, × 450; 12, pycnium of *P. boerhaviaefoliae*, × 400; 13, mesospore, × 800; 14, teliospore, × 800; 15, mature telium showing the elongated plectenchyma cells, × 400.



Figs 9–15

germ pores and borne singly on pedicels. Telia primarily developing within the uredia, later formed separately, white and fluffy, subepidermal, acervulus-like, erumpent, teliospores clavate, rounded at both ends, measuring 30–41 × 7–8.5 μ pedicellate, germinating intrasorum by prolongation of spore apex, promycelium semi-internal, first wall being laid within the middle of the teliospore region, four-celled, sporidia formed by rounding up of the cells of the promycelium, fragile, easily separating and measuring 5–8.5 × 7–8 μ. Pedicels hyaline, persistent, elongating up to 48 μ, pushing the germinating teliospores above the level of the non-germinated spores.

Hab. On leaves of *Ichnocarpus frutescens* Br., Yashavantapur (Mysore), 14–8–1942, leg. M. J. Thirumalachar (Type). Type deposited in the author's herbarium, Herb. Crypt. Ind. Orient. of the Imperial Agric. Res. Inst. New Delhi; Arthur Herbarium, Purdue University, Lafayette, Indiana, U. S. A. and in the herb. of the Imperial Mycological Institute, Kew, England.

Puccinia Volutarellae Thirumalachar, sp. nov.

Telia hypophylla, raro amphigena, subepidermalia, minuta, sparse distributa, aparaphysata atque nigra, soris tenuiter pulvinatis; teliosporae ovatea vel ellipsoidae, brunneo-luteae, rotundatae, in utroque apice, tenuiter constrictae in septis, minute atque delicate verruculosae, magnitudinis 28–44 × 17–24 μ.

Habitat in foliis vivientibus *Volutarellae divaricatae* Benth. 28–12–1942, in loco Bellur, in regione Mysore; leg. M. J. Thirumalacher. Typus positus in Herb. Crypt. Ind. Orient, New Delhi.

Telia hypophyllous, rarely amphigenous, subepidermal, minute, sparsely distributed, aparaphysate and black, sori slightly pulvinate; teliospores ovate to ellipsoid, yellowish-brown, rounded at both ends, slightly constricted at the septa, minutely and finely verruculose, measuring 28–44 × 17–24 μ.

Hab. On living leaves of *Volutarella divaricata* Benth., 28–12–1942, Bellur, Mysore State, leg. M. J. Thirumalachar. Type deposited in the Herb. Crypt. Ind. Orient New Delhi (FIG. 9).

Only telia of this rust have so far been observed. The infection spots are not visible on the upper surface, the sori which are black being as a rule hypophyllous. There are no paraphyses within the sori which are somewhat pulvinate. It differs from the other rusts

so far recorded on the Compositae. Mature teliospores germinate after a period of rest when placed in moist chambers. The promycelium is four-celled, bearing globular sporidia.

Puccinia bellurensis Thirumalachar, sp. nov.

Uredia amphigena, per folia atque culmos dispersa, minuta, pulverulenta atque aparaphysata; urediosporae oblongo-ellipsoidae, subglobosae, pallide luteae, tenuiter brunneae tinctae, episporio minute atque delicate papillato, duobus germinationis poris instructae, magnitudinis 18–24 × 17–20.5 μ. Telia saepissime caulina, orta post amotas urediosporas quarum locum occupant, teliosporae 2-cellulatae, castaneo-brunneae, leves, tenuiter constrictae in septis obtusae in utroque apice, sporarum apice crasso, magnitudinis 33–43 × 17–23 μ. Pediculis hyalinus, persistens, ad 36 μ. longus.

Habitat in foliis *Evolvuli alsinoidis* L. in loco Bellur (Mysore), 28–12–1942, leg. M. J. Thirumalachar. Typus positus in Herb. Crypt. Ind. Orient, New Delhi.

Uredia amphigenous, distributed on leaves and stems, minute, pulverulent, and aparaphysate; urediospores oblong-ellipsoid, subglobose, pale yellow with brownish tinge; epispore minutely and finely papillate with two germ pores and measuring 18–24 × 17–20.5 μ. Telia mostly cauline, developed by replacing the urediospores; teliospores two-celled, chestnut-brown, smooth, slightly constricted at the septa, pointed at both ends, spores slightly thickened at the apex, measuring 33–43 × 17–23 μ. Pedicel hyaline, persistent, up to 36 μ long (FIGS. 10 and 11).

Hab. On leaves of *Evolvulus alsinoides* L., Bellur, 28–12–1942, leg. M. J. Thirumalachar. Type deposited in the Herb. Crypt. Ind. Orient, New Delhi.

P. bellurensis does not bear any resemblance to *Puccinia tuyutensis* Speg. recorded on *Evolvulus falcata* and *E. glabra* in South America, because it has deep yellowish brown and smooth urediospores as against pale yellowish brown and minutely papillate urediospores of the present rust. Furthermore the teliospores of *P. tuyutensis* are broader (22–28 μ) than those of *Puccinia bellurensis* which are 17–23 μ. As specimens of *Uredo Evolvuli* Speg., which is also reported from South America, are not available for comparison and since its telial stage is unknown, its status will have to remain uncertain for the present.

Puccinia boerhaviaefoliae Thirumalachar, sp. nov.

Pycnia amphigena, subepidermalia, citro-lutea. Aecia amphigena, dense aggregata, in infectionis maculis, cupulata, erumpentia, peridio bene evoluto; aeciosporae luteae, polyhydrales, minute verruculosae, magnitudinis, 15–21 × 10–17 μ. Peridii cellulae amplae, hyalinae, angulariter globoidae, dense rugosae. Telia ut plurimum in culmis, initio citro-lutea, tum nigra, atque erumpentia, in distinctis loculi efformatis elongato plectenchymate vallo simili; teliosporae pedicellatae, tenuiter constrictae in septis, castanneo-brunneae, rotundatae vel attenuatae in apice, leves, magnitudinis 34–46 × 12–19 μ. Pediculo persistente, luteobrunneo, ad 20–36 μ longo; mesosporis associatis, magnitudinis 19–36 × 8.5–19 μ.

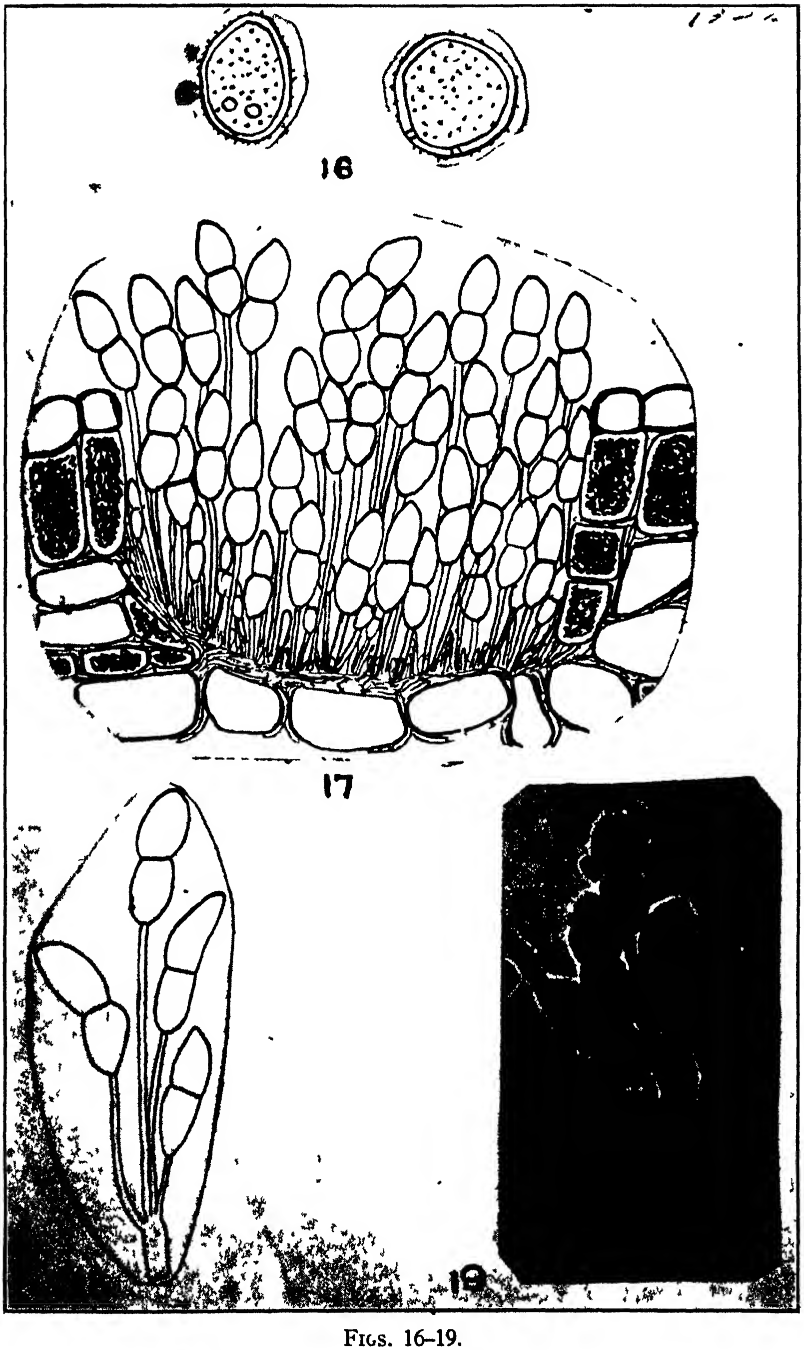
Hab. in foliis atque virgultis *Blepharidis boerhaviaefoliae* Pers. in loco Yashavantapur, 14–8–1942, legit M. J. Thirumalachar. Type deposited in the Herb. Crypt. Ind. Orient, New Delhi.

Pycnia amphigenous, subepidermal, orange-yellow. Aecia amphigenous, densely aggregated on the infection spot, cupulate, erumpent, with well developed peridia; aeciospores yellow, polyhedral, minutely verruculose, measuring 15–21 × 10–17 μ. Peridial cells large, hyaline, angularly globoid, densely rugose, measuring 21–29 × 14–25 μ. Telia mostly on the stem, orange-yellow in early stages, later black and erumpent, in distinct locules formed by the elongated palisade-like plectenchyma; teliospores pedicellate, slightly constricted at the septa, chestnut-brown, rounded or attenuated at the apex, smooth, measuring 34–46 × 12–19 μ. Pedicel persistent, yellowish brown, up to 20–36 μ long, mesospores associated, measuring 19–36 × 8.5–19 μ.

Hab. On leaves and twigs of *Blepharis boerhaviaefolia* Pers., Yashavantapur, 14–8–1942, leg. M. J. Thirumalachar (FIGS. 12–15).

Comparative studies of the aecia of *Puccinia boerhaviaefolia* and *Aecidium Blepharidis* Har. & Pat. (collected by McRae near Coimbatore and identified by Sydow (**1914**) obtained from the Herb. Crypt. Ind. Orient, New Delhi, indicated that the two rusts are identical. Average of 100 spore measurements for the two rusts is as follows: 17.3 × 14.5 μ for the aeciospores of *P. boerhaviaefoliae*, and 17.3 × 14 μ for the rust collected by McRae. *Puccinia Blepharidis* P. Henn., which was recorded by Hennings

FIG. 16, urediospores of *Puccinia Solmsii*, × 800; 17, mature telium, × 560; 18, showing the teliospore cluster on sporogenous basal cell, × 640; 19, photomicrograph of the same, × 600.



FIGS. 16–19.

from Africa, has also been described by Doidge (1926). Recently another rust on the same host species, *Blepharis boerhaviaefolia*, has been described by Cummins (1941) under the name *Puccinia makenensis* Cumm. The latter rust somewhat resembles *P. Blepharidis*, but differs in possessing loculate paraphysate telia. In the rust under study also there is such a loculate telium, and comparison with the photomicrographs given by Dr. Cummins indicates that they doubtlessly develop in the same manner. However, a close morphological study of the development of the sori by the writer revealed that the tissue separating the locules should not be considered to be of the nature of paraphyses. The young telial initial is formed by the concentration of hyphae beneath the epidermis to form a plectenchyma. Soon, an elongated vertical row of cells are arranged in a palisade-like manner. Teliospores that are formed from the base of the hymenium push apart these palisade-like hyphal cells and in the mature telium a loculate appearance for the sorus is presented. It is possible that even in *P. makenensis* the hyphal tissue separating the locular telium might be of the same nature.

Loculate telia no doubt distinguish *P. makenensis* and *P. boerhaviaefoliae* from *P. Blepharidis*. When the spore measurements of these three rusts are taken into account, the following facts become apparent:

	Aeciospores	Peridial cells	Teliospores
P. Blepharidis (E. M. Doidge)	15–22 × 12–19 µ	16–20 × 10–16 µ	35–58 × 18–28 µ
P. boerhaviaefoliae			
P. makenensis (Cummins)	13–17 × 17–20 µ	14–20 × 16–26 µ	48–66 × 17–27 µ

The measurements, while indicating close relationships between the three rusts as regards aeciospore measurements, show differences in the sizes of the teliospores and peridial cells. *Puccinia boerhaviaefoliae* has smaller teliospores as compared with the other two rusts. Further, the smaller peridial cells in *Puccinia makenensis* clearly distinguishes it from *P. boerhaviaefoliae*.

PUCCINIA SOLMSII P. Henn.

The rust on *Polygonum chinense* was first described by Hennings under the name *Puccinia Solmsii* P. Henn., having uredial and telial stages. Raciborski (**1900**) while recording the species from Java described an aecial stage for the rust without making any mention of the uredial stages described by Hennings. The Sydows (**1904**), while referring to *P. Solmsii*, state that Hennings might have mistaken the pedicels of the teliospores for urediospores. However, a detailed study of the same rust collected by the writer in Nandi Hills (Mysore State) revealed the presence of both uredial and telial stages of the rust and other interesting features which are presented here.

Only uredial and telial stages of the rust have been observed. The uredia are minute, hypophyllous, developed on small pinkish infection spots. The urediospores are oblong-elliptic, cinnamon-brown, minutely and finely verruculose, with two distinct germ pores (FIG. 16). Telia are developed (FIG. 17) on slightly raised pulvinate infection patches, amphigenous and subepidermal. The teliospores arise in clusters on proliferating basal cells which are laterally free. There are six to eight spores in a cluster (FIGS. 18 and 19) and these can be made out only in carefully teased preparations. Mature teliospores are two-celled, thin-walled, pale yellowish brown, with a distinct germ pore in each cell. The spores germinate readily within the sorus without a period of rest being necessary.

The occurrence of clustered teliospores on laterally free sporogenous basal cells is a very distinguishing character of rust genera like *Chaconia* Juel, *Scopella* Mains and others. In fact in the possession of two-celled teliospores on sporogenous basal cells, the present rust can be compared with *Coniostelium* Syd. and *Prospodium* Arth. But unlike these two genera, the urediospores are borne singly on pedicels and not in clusters. Further, the sporogenous basal cells are so fragile that the clustered nature could be made out only in carefully prepared sections. For the present, the rust is retained under *Puccinia* as P. *Solmsii* P. Henn.

UROMYCES MUCUNAE Rabenh.

Uromyces Mucunae Rabenh. was first described by Rabenhorst as being parasitic on the leaves of *Mucuna puriens* DC., on the basis of the material collected by Kurz in the Botanical Gardens, Calcutta (India). It is now known to occur on other species of *Mucuna* including *M. utilis* or the velvet beans (Doidge, 1926). Only uredia and telia are so far known for the rust.

Since the rust occurs in profusion round about Bangalore, opportunity was taken to study the morphology of the spore forms including its life-cycle. Uredia are hypophyllous, scattered over the entire surface of the leaves, the urediospores being hyaline with densely echinulate exospore and possessing four scattered germ pores. The telia which replace the uredia are brownish black. The teliospores are chestnut-brown with a blackish tinge, globose, with an apical indistinct germ pore. The exospore shows a large number of warts which are arranged in longitudinal rows, making the spores appear somewhat striate. The teliospores germinate only after a period of rest.

Mature teliospores which were collected and stored in the laboratory readily germinated after a three months rest period, when placed in moist chambers. The promycelium becomes recurved, bearing four globular basidiospores. Germinating teliospores were placed on young leaves of *Mucuna puriens*, the inoculated plants being inclosed in moist chambers for 24 hours. Development of pycnia in the inoculated area after ten days as greenish yellow specks indicated the autoecious nature of the rust. Pycnia are emphigenous, subepidermal, flask shaped with well developed ostiolar hyphae. Uredia follows pycnia in development. The urediospores readily germinate and bring about secondary infection.

In conclusion the writer wishes to acknowledge his indebtedness to Dr. B. B. Mundkur, Imperial Agricultural Research Institute, New Delhi, for guidance and valuable suggestions given in the course of this work. Grateful thanks are due to Dr. L. N. Rao, Professor of Botany, University of Mysore, for kind encouragement and to Rev. Father H. Santapau, Ph.D., S.J., St. Xavier's

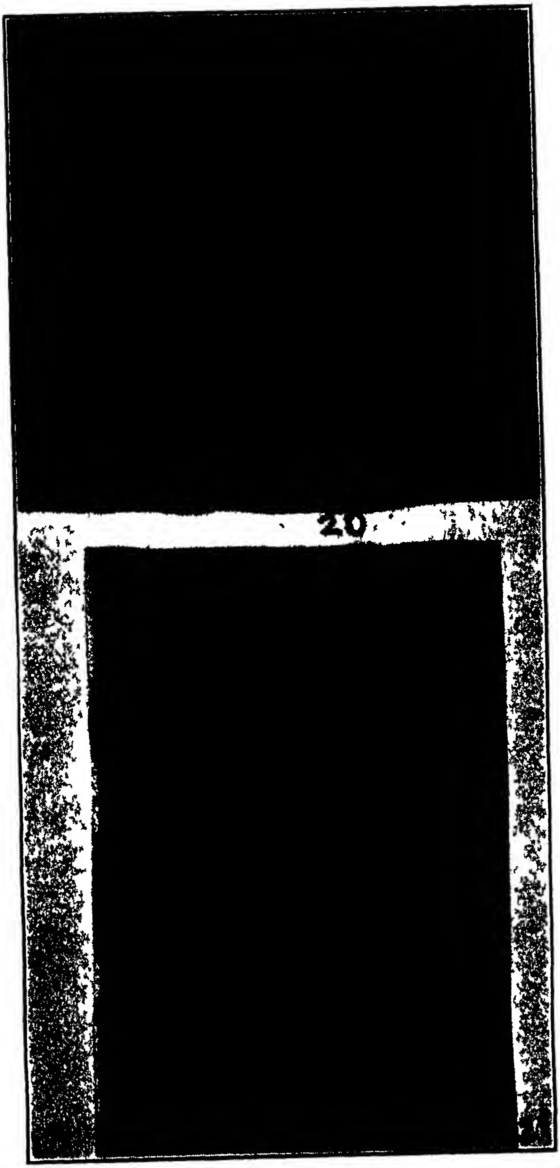


FIG. 20, photomicrograph of the telium of *Acervulopsora Ichnocarpi*, × 450, 21, photomicrograph of the germinating teliospores showing the fragile promycelium in the extreme right spore and rounding off of the spores in the others, × 800.

College, Bombay, for kindly writing the Latin diagnosis of the new genus and species.

DEPT. OF BOTANY,
CENTRAL COLLEGE,
BANGALORE, INDIA

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SOME NEW SPECIES OF FUNGI ON LIBOCEDRUS

Edith K. Cash

(with 5 figures)

Among collections of Discomycetes from California referred to the writer at various times during recent years have been several specimens of fungi growing on *Libocedrus decurrens* Torr. which are apparently distinct from any of the species described in the available literature and are therefore described here as new. One discomycete and an associated Sphaeropsidaceous fungus on branchlets have been collected by H. E. Parks along the Middle Fork of the Smith River, Del Norte County, several times from 1936 to 1945. Another discomycete on bark of *Libocedrus* has been found at various localities in the state by L. Bonar, C. R. Quick, E. P. Meinecke, and C. L. Shear.

Specimens of these fungi are deposited in the Mycological Collections of the United States Bureau of Plant Industry, Beltsville, Maryland, and in the Herbarium of the University of California, Berkeley, California.

1. **Parksia** gen. nov.

Apothecia superficialia, carnoso-coriacea, depresso-globosa, in lobis pluribus scindentia, dein plana vel convexa margine stellato; asci cylindrico-clavati, octospori; ascosporae hyalinae, unicellulares; paraphyses filamentosae, flexuosae; hypothecium crassum, subhyalinum plectenchymaticum; cortex fuscus, pseudoparenchymaticus.

Apothecia superficial, fleshy-leathery, depressed-globose, opening by splitting into lobes, then plane or convex with stellate margin; asci cylindrical-clavate, 8-spored; spores hyaline, ellipsoid, one-celled; paraphyses filamentous, flexuous; hypothecium thick, subhyaline, plectenchymatous; cortex dark, pseudoparenchymatous.

The genus is named for Mr. Harold E. Parks, to whose keen interest in the fungus flora of California the writer has been indebted for many valuable collections.

Parksia Libocedri sp. nov. (FIG. 1 and 4)

Apothecia substipitata, superficialia, 0.5–1 mm. diam., depresso-globosa, dein in lobis pluribus scindentia et plana vel convexa margine lobato, carnoso-coriacea, fusco-brunnea usque cinnamomeo-brunnea; hymenium olivaceo-citrinum; asci cylindrico-clavati, octospori, 90–110 × 8–11 μ; ascosporae 1–2-seriatae, ellipsoideo-ovoideae, unicellulares, hyalinae vel subhyalinae, 9–11 × 3–5 μ; paraphyses hyalinae, tenues, filamentosae, ramosae, apice inflatae et viridescentes; hypothecium subhyalinum, plectenchymaticum; cortex pseudoparenchymaticus, cellulis fuscis angularibus crasse tunicatis 5–7 μ in diam. compositus.

Apothecia substipitate, single or crowded, emerging from black hyphae on the stem of the host between the leaves, superficial, 0.5–1 mm. in diameter, at first depressed-globose, opening by splitting from the apex into 8–10 lobes and expanding into a plane or convex disk surrounded by the stellate lobes of the exciple, fleshy-leathery, exterior bone brown [1] at the base, cinnamon brown to clay-color on the marginal lobes, hymenium yellowish citrine or old gold to light brownish olive, drying Natal brown to bone brown; asci cylindrical-clavate, long-pedicellate, 8-spored, 90–110 × 8–11 μ; spores in the upper part of the ascus, obliquely uniseriate below to biseriate above, ellipsoid-ovoid, straight or slightly curved, unicellular, biguttulate, granulose, hyaline to yellowish, 9–11 × 3–5 μ; paraphyses hyaline, fine, filamentous, flexuous, branched, exceeding the asci, swollen and greenish at the apex; hypothecium subhyaline to pale brown, plectenchymatic, 100–150 μ thick, extending over the inner surface of the marginal lobes; cortex pseudoparenchymatic, composed of black, thick-walled, angular to subcircular cells 5–7 μ in diameter.

On branchlets of *Libocedrus decurrens* Torr., California; along the Middle Fork of the Smith River, Del Norte Co., Mar.–Apr. 1936, H. E. Parks *5604*; Nov. 1937, *6120*; Jan. 1938, *6039, 6121,* and *6134* (*Type*).

The dark, fleshy exciple and stellate opening are characters which place this genus in the Tryblidiaceae, although in Nannfeldt's classification it seems more closely related to the genera included in the section Encoelioideae of the Helotiaceae. Among genera of the Tryblidiaceae the fungus resembles *Heterosphaeria* in its splitting into lobes, but differs from the latter in the thick hypothecial layer made up of very thin, delicate, interwoven

[1] Color nomenclature is that of Ridgway, R. Color standards and color nomenclature. Washington, 1912.

FIG. 1, *Parksia Libocedri* and *Camaropycnis Libocedri* on *Libocedrus decurrens* (× 4); 2, *Camaropycnis Libocedri*, section of pycnidium (× 55); 3, detail of 2 (× 125); 4, *Parksia Libocedri*, section of apothecium (× 55); 5, *Tryblidiella magnispora* on *Libocedrus decurrens* (× 8).

hyphae, while in *Heterosphaeria* the tissue is prosenchymatous, composed of elongate cells with cartilaginous to gelatinous thickened walls. The structure of the apothecium in *Parksia* is similar to that of *Tryblidiopsis;* the latter differs, however, in the large asci, the large two-celled spores, which are surrounded by a gelatinous sheath, and in the apothecia emerging from beneath the bark.

2. **Camaropycnis** gen. nov.

Pycnidia superficialia, subglobosa, ostiolata, levia, carnoso-coriacea, e parietibus tenuibus in loculos multos, subsphericales divisa; conidia hyalina, unicellularia, e conidiophoribus hyalinis, subulatis, singulatim oriunda.

Pycnidia superficial, subglobose, ostiolate, smooth, fleshy-leathery, divided by thin walls into many subglobose locules; conidia hyaline, unicellular, borne singly on unbranched, hyaline, subulate conidiophores.

Camaropycnis Libocedri sp. nov (FIG. 1, 2, and 3)

Pycnidia superficialia, sessilia vel substipitata, subglobosa, levia, atrobrunnea, 0.7–1 mm. in diametro et altitudine, ostiolata, carnoso-coriacea, in loculos numerosos subsphericales 50–100 μ in diam. divisa; conidiophora simplicia, eseptata, tenuia, subulata, 5–6 × 0.5–0.7 μ; conidia cylindrica, hyaline, unicellularia, 14–15 × 2–2.5 μ.

Pycnidia superficial, sessile to substipitate, developing from a black, felty hyphal base embedded between the leaves of the host, subglobose or depressed-globose, nearly smooth and bone brown to Natal brown when moist, black and much wrinkled, furrowed or pitted when dry, 0.7–1 mm. in height and diameter, fleshy to leathery; ostiole papillate, apical or excentric, usually single, but occasionally two to a single pycnidium; wall 25–35 μ thick, the outer layer black pseudoparenchymatous, of small, angular, thick-walled cells, 5–10 μ in diameter, the underlying layers hyaline, gradually changing to a plectenchymatous tissue which fills the stem-like base and divides the interior of the pycnidium into many layers of subspherical locules 50–100 μ in diameter; conidiophores lining the locule walls, unbranched, continuous, thin, delicate, subulate, 5–6 × 0.5–0.7 μ; conidia borne singly, cylindrical, hyaline, unicellular, rounded at the ends, 14–15 × 2–2.5 μ, contents granulose; walls of the locules extremely delicate and evanescent, leaving the conidia aggregated into closely compact, globular masses; spore globules after expulsion from the ostiole often collecting on the exterior and giving the pycnidium a white-dotted appearance.

On branchlets of *Libocedrus decurrens* Torr., California: along the Middle Fork of the Smith River, Del Norte Co., Mar.–Apr. 1936, H. E. Parks *5604-A*; Nov. 1937, *6120-A*; Jan. 1938, *6039-A, 6121-A*, and *6134-A* (*Type*); June 1939 and Jan. 16, 1945 (unnumbered); Palomar, San Diego Co., May 6, 1939, C. L. Shear.

The development of *Camaropycnis Libocedri* on the same branchlets as the ascomycete, *Parksia Libocedri*, from a similar black hyphal base embedded between the leaves, and the resemblance of the dark cortex and thick hyaline underlying tissue in the two fungi, suggest that they may possibly be stages in the life history of a single species. Cultures from these specimens, however, failed to develop, and there is therefore no cultural evidence that the fungi are related.

A stipitate discomycete frequently found on the same twigs with both *Parksia Libocedri* and *Camaropycnis Libocedri* has been tentatively referred to *Kriegeria*. In macroscopic appearance and the shape and dimensions of the spores it agrees with *K. Jacksoni* Seaver (*Chloroscypha Jacksoni* Seaver) which has been recorded, however, only on species of *Thuja*. It is possible that the fungus may be *Peziza alutipes* Harkn. (*Phialea alutipes* (Harkn.) Sacc.), but no material of this species has been available for comparison. The type is not in the Harkness Herbarium at the California Academy of Sciences in San Francisco, and the identity of the species can not be definitely determined.

3. **Tryblidiella macrospora** Bonar & Cash, sp. nov. (FIG. 5)

Apothecia erumpentia, sessilia, singula vel 2–3-caespitosa, carnoso-coriacea, atra, depresso-globosa, 0.7–1 × 0.5–1 mm., 0.5–0.7 mm. alta, rima longitudinali vel 3–4 lobis aperientia; asci late clavati, breviter stipitati, 150–230 × 55–65 μ, apice crasse tunicati, plerumque 8-spori, rarius 2–4-spori; ascosporae 2–3-seriatae, fuscae, uniseptatae, late ellipsoideae, medio constrictae, 50–70 × 25–33 μ; paraphyses numerosae, filiformes, in epithecium fuscum agglutinatae; hypothecium prosenchymaticum, brunneum, e strato plectenchymatico, crasso, subhyalino distincte definitum; cortex ater, coriaceus, pseudoparenchymaticus.

Apothecia sessile, erumpent from a stromatic base beneath the bark, closely and evenly distributed, either singly or in groups of two to three, fleshy-leathery, black, round to elliptical in outline, 0.7–1 × 0.5–1 mm. by 0.5–0.7 mm. high, opening by a longitudinal

slit or more often by three or four lobes, margin inrolled, lobate; exciple consisting of a black, leathery layer 25–40 μ thick, pseudoparenchymatous on the surface, merging into a thick, subhyaline plectenchyma up to 150 μ thick near the base, narrower toward the margin; hypothecial layer prosenchymatic, brown, sharply defined from the underlying plectenchyma; asci broad-clavate, short-stipitate, 150–230 × 55–65 μ, the wall gelatinous and thickened at the apex to 10–15 μ, opening by a pore, 8- (rarely 2- or 4-) spored; ascospores irregularly 2–3-seriate, dark brown, uniseptate, broad ellipsoid, constricted at the septum, each cell with a conspicuous flask-shaped gutta, germinating spores with a hyaline papilla at each end, 50–70 × 25–33 μ; paraphyses numerous, filiform, much branched, dark brown at the apex and agglutinated into a thick epithecium.

On bark of *Libocedrus decurrens* Torr., California: Pineridge, Fresno Co., Sept. 6, 1921, L. Bonar (*Type*); Stanislaus National Forest, Tuolumne Co., June 3, 1941, C. R. Quick; Feather River Experiment Station, near Quincy, Plumas Co., Oct. 15, 1917, E. P. Meinecke; Palomar, San Diego Co., May 5, 1939, C. L. Shear.

The fungus is closely related to *Caldesia Sabinae* (De Not.) Rehm described on *Juniperus* in Europe, from which it differs in the much larger spores, as well as in the host. In European material examined the largest spores found were 38 μ long, while the shortest in the California specimens measured 50 μ, ranging up to 70 μ in length.

Von Hoehnel (2) has pointed out that *Tryblidium Sabinae* De Not. does not belong to *Caldesia* Trevisan, which is a genus of lichens, and that *Caldesia* in the sense of Rehm is therefore invalid as a generic name. Von Hoehnel referred *Caldesia Sabinae* (De Not.) Rehm to *Eutryblidiella*, raising Rehm's section to generic rank to include the species of *Tryblidiella* having two-celled spores. Later Nannfeldt (3, p. 333–334) combined the species as *Tryblidiella Sabinae* (De Not.) Nannf., placing both *Eutryblidiella* (Rehm) Hoehn. and *Caldesia* Rehm (non Trev.) as synonyms of *Tryblidiella*. It is also stated by Butler (1, p. 821) that *Caldesia Sabinae* "is without doubt closely related to *Tryblidiella rufula*."

For the present, the new species on *Libocedrus* is referred to *Tryblidiella* in conformity with the disposition of the allied species,

T. Sabinae. The spores and asci of both species are unquestionably similar to those species of that genus with two-celled, constricted spores, like *T. hysterina* (Duf.) Shear. In both *T. Sabinae* and *T. macrospora* the apothecia are more deeply seated in the host, emerging only slightly abover the surface of the bark, not superficial and substipitate as is often the case in mature apothecia of *Tryblidiella.* The splitting of the apothecial margin is also different from that described for species of the genus. The even margin of *Tryblidiella* is a feature noted by Rehm (**4**, p. 233) as contrasted with the lacerate opening of *Tryblidium.* It is a question, therefore, whether *Caldesia* sensu Rehm should not be given a new name and retained as a distinct genus.

UNITED STATES PLANT INDUSTRY STATION,
BELTSVILLE, MARYLAND

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OBSERVATIONS ON CERTAIN SPECIES OF USTILAGO ON HILARIA, STENOTAPHRUM, AND MUHLENBERGIA [1]

George W. Fischer and Elisa Hirschhorn [2]

(with 2 figures)

Ustilago affinis Ellis & Ev. In Cockerell, T. D. A., Bull. Torrey Club **20**: 297. 1893.

Ustilago Stenotaphri P. Henn. Hedwigia **37**: 293. 1898.

Ustilago Stenotaphri Mass. Kew Bull. **1899**: 184. 1899.

Ustilago americana Speg. Anal. Mus. Nac. Buenos Aires **6**: 207. 1899.

Ustilago Henningsii Sacc. & Syd. In Sacc. Syll. Fung. **16**: 368. 1902.

Sori in the inflorescence 4–10 mm. long, dark-brown, very dusty, soon exposing the naked rachis, but at first covered with a thin, very fragile, grayish membrane (fig. 2, B).

Spores clear yellowish-brown, globose or irregularly globose to ovoid, or somewhat angular, 4–7 μ in diameter, or 4–5 $\times$ 7–8 μ; epispore very thin, smooth (fig. 1, F).

On Graminaeae:

Stenotaphrum glabrum Trin. Argentina: Uruguay.

Stenotaphrum secundatum (Walt.) Kuntze. Puerto Rico.

Ustilago affinis var. **Hilariae** (P. Henn.) G. W. Fisch. & Hirsch. comb. nov.

[1] Investigations of the smut diseases of grasses, cooperative between the Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, and the Washington Agricultural Experiment Station, Pullman, Washington. Published as Scientific Paper No. 600, College of Agriculture and Agricultural Experiment Station, State College of Washington.

[2] Pathologist, Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture, and Assistant in Plant Pathology, State College of Washington, respectively.

Ustilago Hilariae P. Henn. Hedwigia **37**: 267. 1898.

Spores yellowish brown to brown, globose to subglobose, 6–9 μ in diameter, or 6–7 × 9–10 μ; epispore thin, punctate to slightly echinulate (FIG. 1, E and 2 A).

On Gramineae:

Hilaria Belangeri (Steud.) Nash. U. S.: Texas.
Hilaria cenchroides H.B.K. U. S.: Texas, New Mexico.

Ellis and Everhart's original description (**5**) of *Ustilago affinis* is very meager, so much so in fact that the species is almost a *nomen nudum*. However, subsequent descriptions by Clinton (**3**, **4**) and others seem to have established a definite concept of this species. These authors all describe *U. affinis* as having smooth spores.

Ustilago affinis has been considered as attacking *Hilaria* and *Stenotaphrum*. In the material which we have examined we find consistently that on *Stenotaphrum* the spores are smooth (FIG. 1, F) and on *Hilaria* they are punctate to minutely echinulate (FIG. 1, E) as seen under oil immersion.

Hennings (**7**) considered the *Hilaria* smut as distinct and gave it the name *U. Hilariae* with the following description: "Soris in spiculis, atris, membrana alkida subvelatis; sporis subglobosis, flavo-brunneolis 1–2 guttulatis 6–8 μ, episporis levi, brunneo. Mexico, bei der Stadt Mexico in Aehren von *Hilaria cenchroides* Oct. 1896. (Holway)."

Hennings' *Ustilago Hilariae* has been considered by other investigators as a synonym of *U. affinis,* probably on the basis of Hennings' description of the spores as smooth, and also their failure to examine with the oil immersion lens. Since, however, we find that the spores on *Hilaria* are punctate to slightly echinulate, besides being slightly larger and darker, we are inclined to consider the smut on *Hilaria* as a different entity and have accordingly proposed the variety named above. Since the specimens on *Hilaria* correspond quite well to Hennings' *U. Hilariae* we have used his name for the variety.

According to Spegazzinni (**10**) and Ciferri and Herter (**1**), *Ustilago Stenotaphri* McAlp. (**9**) is another synonym of *U.*

affinis. It is clearly evident, however, from McAlpine's description and illustrations of his species that it cannot possibly be included in the synonymy of *U. affinis*. It appears that McAlpine's *U. Stenotaphri* is a valid species with large irregular dark-brown spores, 10–13 × 16–17 μ.

Specimens examined: on *Hilaria Belangeri,* San Antonio, Texas, 5–16–41, leg. H. W. Johnson, fid. G. W. Fischer No. *358,* Myc. Coll. Bur. Pl. Ind. No. *85212;* on *H. cenchroides,* Dublan, Mexico, 9–4–05, Griffiths' Coll. in Brooklyn Bot. Gard. Herb.; *ibid.,* Spoffard, Texas, 5–8–05, Griffiths' Coll. in Brooklyn Bot. Gard. Herb.; on *H. Belangeri,* San Antonio, Texas, 4–24–40, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* Sonora, Texas, 7–16–36, in Myc. Coll. Bur. Pl. Ind.; on *Stenotaphrum secundatum,* Dries, Puerto Rico, 6–4–37, in Myc. Coll. Bur. Pl. Ind.; *ibid.,* San Juan, Puerto Rico, 1–19–43, leg. and fid. L. J. McConnell, San Juan No. *8465.*

USTILAGO MUHLENBERGIAE P. HENN. AND USTILAGO MUHLENBERGIAE CLINT.

During a recent study of herbarium material under the designation of *Ustilago Muhlenbergiae* P. Henn. it has become obvious that two distinct species have been distributed in the exsiccati under this name. Both species have much the same macroscopic characters, but in one the spores are clear, light brown, and prominently echinulate, especially at the poles (which are nearly hyaline). The other species has smooth, opaque, dark-brown spores provided with cap-like appendages at opposite ends or with the exospore grooved to form the unopened appendages.

In 1902 Hennings (8) described an inflorescence smut on *Muhlenbergia Pringlei* (a synonym for *M. pauciflora*) as *Ustilago Muhlenbergiae*. Hennings' original description follows:

"Soris paniculas destruentibus tumefacientibusque, oblonge ovoideis, 3–6 mm. longis, 2–3 mm. latis, diutuis epidermide, flavocinerescente tectis, duris, dein atris pulverulentis; sporis globosis vix acutangulis, fuscis 4–4.5 μ diam., episporio atro-fusco, levi."

Also in the same year Clinton (2) described an inflorescence smut on *Muhlenbergia texana* as *Ustilago Muhlenbergiae*. Clinton's original description follows:

"USTILAGO MUHLENBERGIAE Clint. n. sp.—Sori in the inflorescence, ovoid to subspherical, about 3–6 mm. in length, protected by thin, semi-transparent membrane of the infected enveloping glumes, upon rupture disclosing black-brown dusty spore mass;

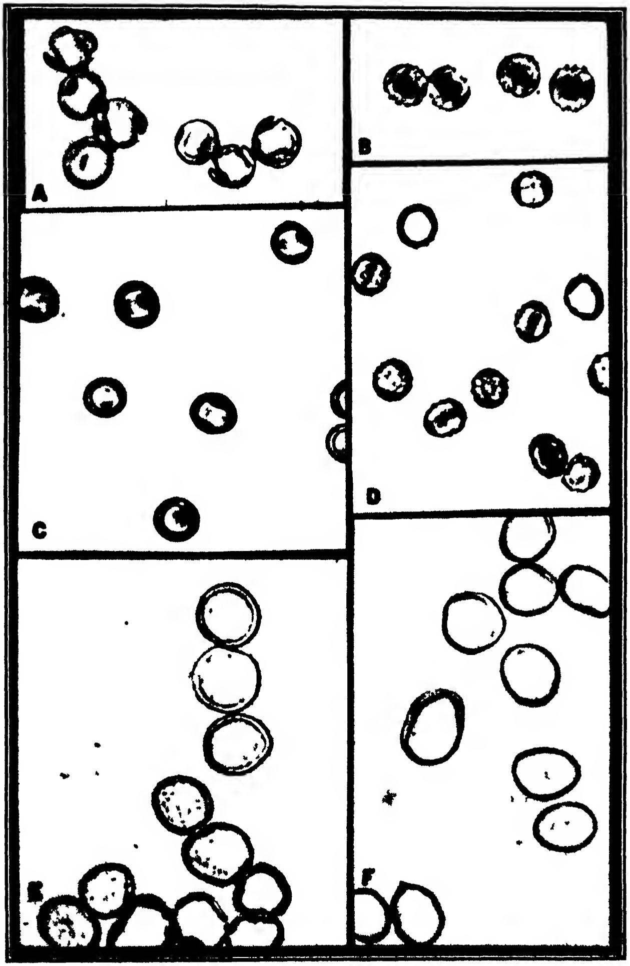

FIG. 1. A, *Ustilago Muhlenbergiae*, chlamydospores, with cap-like appendages; C, *ibid.*, without appendages open, but seen differentiated in the epispore; B, *U. hyalino-bipolaris* from *Muhlenbergia Porteri* (type material of *U. Muhlenbergiae*, ex Herb. W. G. Farlow, leg. Pringle), S. Arizona, Aug. 1884; D, *ibid.*, Santa Rita Mts. Ariz. (Griffith's Coll. No. 368, ex Herb. Brooklyn Bot. Gard.); E, *U. affinis* var. *Hilariae*, from *Hilaria Pelangeri*, Texas; F, *U. affinis*, from *Stenotaphrum secundatum*, Puerto Rico, × approx. 1000.

spores rather dark reddish brown, chiefly spherical, with brittle epispore that breaks up into very small granular echinulations (especially at opposite sides of the spore thus leaving a darker less broken central band) 4–6 μ in diameter.

"Host: *Muhlenbergia texana,* Ariz. (type)."

In a later work Clinton considered his binomial and Hennings' as applying to the same smut, and since Hennings' name appeared a few months earlier, priority was given to *Ustilago Muhlenbergiae* P. Henn. It seems obvious, however, that in these later works (**3, 4**) Clinton combines into one description of *U. Muhlenbergiae,* the characters of two species:

". . . spores rather dark reddish-brown, chiefly spherical, at first apparently smooth, but with age or approaching germination splitting off caps on opposite sides of epispore and these breaking up into small granular echinulations thus leaving a dark, less broken central band, 4–6 μ in diameter."

From the above it is apparent that there are two distinct smuts under consideration. The one, with the smooth, dark, opaque, appendaged spores (FIG. 1, A), corresponds most closely to *Ustilago Muhlenbergiae* P. Henn. and the other with echinulate spores, hyaline at opposite poles (FIG. 1, B and D) to *U. Muhlenbergiae* Clint. Hennings makes no mention of appendages in his description and it seems desirable to amend his description accordingly:

USTILAGO MUHLENBERGIAE P. Henn. Hedwigia **41**: 71. 1902. Amend.

Sori in the abortive inflorescence, black, somewhat gall-like, with a thin hyaline membrane of host tissue, more or less indurate.

Spores dark reddish-brown, opaque, globose to subglobose, 4–6 μ in diameter; epispore smooth, but provided more or less with a definite pattern of grooves which often form cap-like appendages at opposite poles (FIG. 1, A and C and FIG. 2, D).

On Gramineae:

Muhlenbergia pauciflora Buckl., (*M. Pringlei* Scribn.). New Mexico.

Muhlenbergia sp. Arizona.

FIG. 2. A, *Ustilago affinis* var. *Hilariae,* on *Hilaria Belangeri;* B, *U. affinis,* on *Stenotaphrum secundatum,* normal inflorescence on extreme right; C, *U. hyalino-bipolaris,* on *Muhlenbergia Porteri;* D, *U. Muhlenbergiae,* on *M. Pringlei* (*M. pauciflora*). Approximately natural size.

FIG 2

In the specimens examined there appear to be two variations of the epispore. On one, the appendages are well separated from the spore (FIG. 1, A) and are very reminiscent of *Ustilago Williamsii* (Griff.) Hirsch. and G. W. Fisch., a stem smut on *Stipa* and *Oryzopsis* (6). In the other type the cap-like appendages seem outlined on the spore but they have not separated from the spore itself (FIG. 1, C). This latter type seems to correspond more closely to Hennings' original description. In fact, the latter type is observed in the exsiccati which corresponds to the type material, if it is not actually so (Seymour and Earle, "Economic Fungi," Supplement C, edited by G. P. Clinton, No. *C142,* on *Muhlenbergia Pringlei,* Hot Springs, New Mexico, Sept. 15, 1896).

The other smut species on *Muhlenbergia,* with the echinulate spores, is Clinton's *Ustilago Muhlenbergiae,* but since this binomial is already occupied it becomes necessary to propose a new name:

Ustilago hyalino-bipolaris G. W. Fisch. & Hirsch. nom. nov.
Ustilago Muhlenbergiae Clint. Jour. Myc. **8**: 133. 1902.

Sori in the abortive inflorescence, dark-brown to black, gall-like, with thin, fragile, transparent membrane of host tissue, granular to somewhat indurate (FIG. 2, C).

Spores pale yellowish to hyaline at the poles, leaving an equatorial brown to dark brown band, globose to subglobose, often appearing laterally compressed to concave, 4–4.5 μ in diameter; epispore echinulate, especially at the clear, lighter-colored polar areas, echinulations less pronounced in the central dark band, and sometimes appearing arranged in rows (FIG. 1, B and D).

On Gramineae:
Muhlenbergia Porteri Scribn. Arizona, New Mexico.

These two small-spored species of *Ustilago* on *Muhlenbergia* are very similar macroscopically (FIG. 2, C and D), but are readily distinguished by their microscopic characters. Since both are gall-like in the abortive inflorescence and have nearly the same hosts, it would be easy to confuse the two without microscopic examination.

Specimens examined: on *Muhlenbergia* sp., foothills of the San Francisco Mts., Flagstaff, Ariz., Biol. Explorations U. S. Dept. Agr., Death Valley (California) Expedition No. *9,* 12–23–1890

(originally determined as *Ustilago microspora* Ellis & Gall., then crossed out and labeled *U minima* Arth., in same handwriting); on *M. pauciflora* (*M. Pringlei*), Hot Springs, New Mex., 9–15–1896, in Seymour and Earle, Economic Fungi, Supplement C, edited by G. P. Clinton, No. *C142,* Coll. E. W. D. Holway; on *M.* ? *Porteri,* Santa Rita Mts., Ariz., Griffiths' Coll. *368*, in Herb. Brooklyn Bot. Gard.; *ibid.,* Las Cruces, New Mex., Griffiths' Coll. No. *255,* Oct. 5, 1904, in Herb. Brooklyn Bot. Gard.; *ibid.*, S. Arizona, Aug. 1884, Coll. Pringle, in Herb. W. G. Farlow (type material of *Ustilago Muhlenbergiae* Clint. = *U. hyalino-bipolaris* G. W. Fisch. & Hirsch.).

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A NEW RHABDOGLOEUM ASSOCIATED WITH RHABDOCLINE PSEUDOTSUGAE IN THE SOUTHWEST

Don E. Ellis and Lake S. Gill [1]

(WITH 2 FIGURES)

In 1922 Sydow (4) described *Rhabdocline Pseudotsugae* Syd. and *Rhabdogloeum Pseudotsugae* Syd. on Douglas-fir (*Pseudotsuga taxifolia* (Poir.) Britt.) from Montana and suggested that the latter is the imperfect stage of the former. A review of the literature reveals only a few references to *Rhabdogloeum* since that time. Dearness (2) reported its presence in a collection from Colorado and at the same time described *Rhabdogloeum abietinum* Dearness on *Abies Fraseri* (Pursh) Poir. from North Carolina. Wilson and Wilson (6) report the occurrence of a conidial stage of *Rhabdocline* that develops in late summer on the upper surface of Douglas-fir needles in America but state that it has not been found in Scotland. Van Vloten (5) considers their imperfect fungus to be *Rhabdogloeum Pseudotsugae* but does not believe it is linked with *Rhabdocline*.

In May 1939, a disease of 1-year-old (1938 origin) Douglas-fir needles, which appeared to be the needle blight caused by *Rhabdocline Pseudotsugae*, was observed in the Graham Mountains, near Safford, Arizona. Examination of the diseased needles revealed the presence of an imperfect fungus that, in some respects, resembled *Rhabdogloeum Pseudotsugae* (3). Needles collected from the same trees about one month later (June 1939) bore fruits of *Rhabdocline Pseudotsugae*, as well as the imperfect fungus. The disease was observed again in the same locality in May 1940.

[1] Formerly respectively Assistant Pathologist and Senior Pathologist, Division of Forest Pathology, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture; now respectively Associate Plant Pathologist, North Carolina Agricultural Experiment Station, Raleigh, and on military furlough.

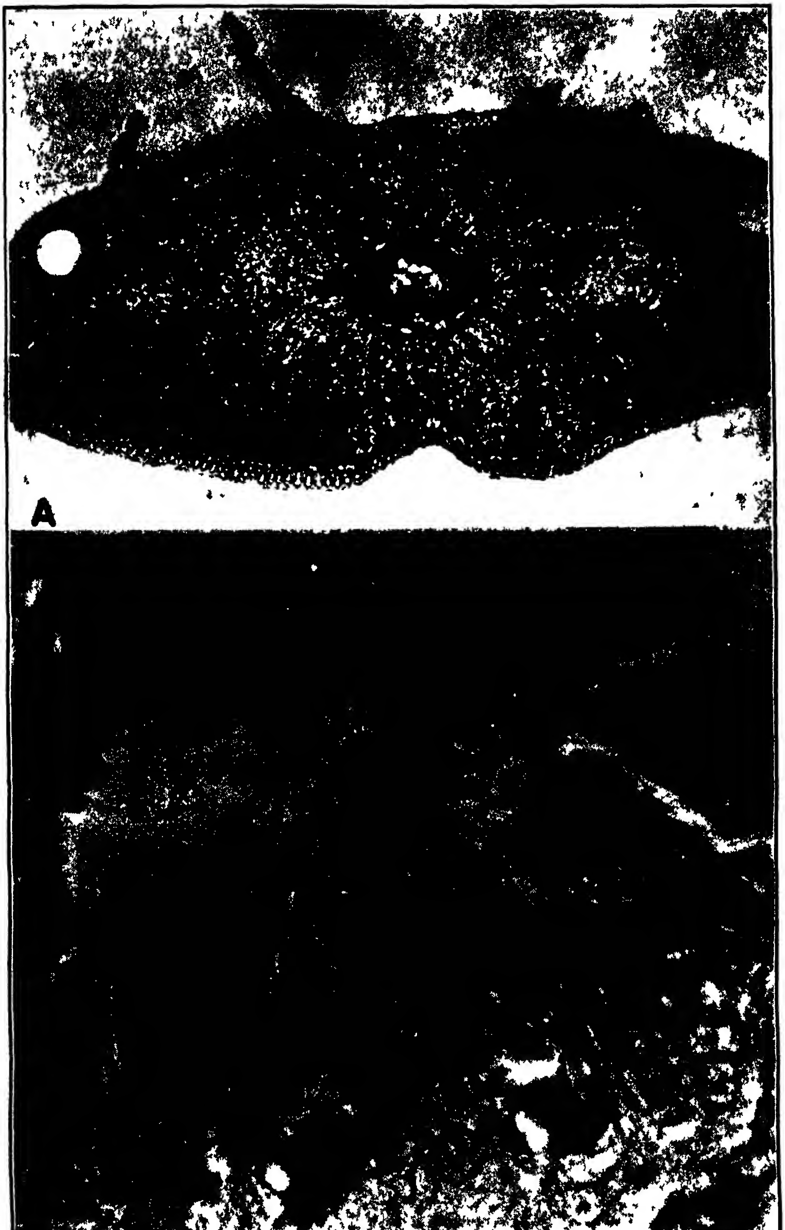

FIG. 1. A, cross section through Douglas-fir needle, showing acervuli of *Rhabdogloeum hypophyllum*, approximately × 75; B, cross section through an acervulus, showing conidia and conidiophores, approximately × 760.

In January 1940, a needle blight that was also similar to the disease caused by *Rhabdocline* was observed on the needles of 1939 origin on young Douglas-fir trees in the Lincoln National Forest near Cloudcroft, New Mexico. No fungus was observed fruiting at that time, but needles from several trees that were placed in moist chambers and kept at room temperature in the laboratory developed numerous acervuli on their lower surfaces within one week. A collection made from the same trees early in March showed the presence of the same imperfect fungus (FIG. 1). Needles from this material, which were kept in a moist chamber at 15–17° C. for about one month, developed mature fruits of *Rhabdocline*. This test was repeated several times during the spring and invariably the imperfect fungus would be supplanted by the perfect one. Additional collections from the same general locality were made at approximately 15-day intervals during March, April, and May. These showed a steady increase in abundance of the imperfect fungus until May when *Rhabdocline* appeared in nature together with conidial form. An additional collection (called to our attention by G. G. Hahn), made by J. S. Hall in the same area in June, was examined and found to contain both mature fruits of *Rhabdocline Pseudotsugae* and the imperfect fungus.

Observations on specimens kept in moist chambers and on material undergoing transition in nature indicate that the asci can originate beneath the conidial layer in the same fruiting structure, apparently forcing the latter out and replacing it as shown in figure 2.

Van Vloten (5) considers *Rhabdocline* to be an obligate parasite and states that he was unable to grow it artificially. We have not attempted to culture *Rhabdocline* but have successfully grown the conidial fungus on artificial media. It was isolated from the diseased needles collected in January 1940, and from each subsequent collection during the spring. The needles were surface-sterilized for two minutes in 1:1000 mercuric chloride, washed in sterile water, and planted on agar. Colonies that developed within the first few days were usually contaminates and had to be discarded. In the case of successful isolations, the hyphae usually issued from the necrotic spots of the leaf after eight or nine days, and not until about a week later did the colonies spread out into the

agar. Subsequent growth was very slow and irregular, the colonies attaining a maximum diameter of only about 18 mm. in one month. The fungus grew on malt, corn meal, and Douglas-fir needle decoction agars, the best results having been attained on the latter. Mycelial growth was sparse, but conidia were produced in abundance, accumulating in masses that formed the most conspicuous part of the colony. On malt agar the colonies were at first white, but with age passed through deepening shades of gray until after one or two months they usually turned dark olive green. Single-spore isolations of conidia produced in culture gave rise to the same type of growth. Although no critical temperature tests have been run, preliminary trials indicate that better growth takes place at room temperature than at temperatures ranging from 1° to 17° C.

The conidia produced in culture are similar to those produced in nature, but in cultures three or more weeks old they are commonly somewhat more constricted in the middle. They often become two-celled at maturity and bear a rather striking resemblance to ascospores of *Rhabdocline*. In old cultures they frequently become thick-walled and dark-colored. In the case of septate spores, one cell often turns dark and the other remains hyaline. Wilson and Wilson (6) noted the same condition in mature ascospores of *Rhabdocline* and state that usually only the dark cell germinates. The conidia usually produce only one germ tube although two-celled spores may produce two. Germination of both hyaline and colored spores has been observed.

The imperfect fungus observed in Arizona and New Mexico resembles *Rhabdogloeum Pseudotsugae* in some respects but the spores are somewhat smaller, the conidiophores are considerably longer, and the underlying hyphal layer from which the conidiophores arise is thicker and more conspicuous. The conidiophores probably more closely resemble those of *R. abietinum* which, according to Dearness (2), are about 45 μ long. In describing *R. Pseudotsugae,* Sydow (4) states, "Konidienträger undeutlich, sehr zart, stäbchenformig, ca. 7–12 × 1.5 μ" whereas in our fungus the conidiophores are prominent, 10–56 × 0.9–2.8 μ (average 28.3 × 1.8 μ). His spore measurements are 15–21 × 4–5 μ, whereas ours are 6.7–11.1 × 2.2–3.7 μ (average 9.1 × 3 μ). We have examined

a portion of the type collection of *R. Pseudotsugae,* as deposited in the Mycological Collections of the Bureau of Plant Industry, Soils, and Agricultural Engineering, and found conidiophores 6.1–14.8 μ (average about 10.1 μ) long and conidia 10.7–17 × 2.9–4.6 μ (average about 14.2 × 3.6 μ). In examining an additional collection (No. *361* Herbarium J. S. Boyce) of *R. Pseudotsugae* from California we found it to conform closely to the type, with conidiophores 6.2–14.8 μ (average about 9.6 μ) long and conidia 11.1–18.6 × 2.8–5.0 μ (average about 14.1 × 3.9 μ). Fruiting bodies were observed on both sides of the needles in the type, but on the upper surface only in the California collection, while in our material fruiting is mainly on the lower, only rarely on the upper surface. The writers, therefore, believe that the conidial form found associated with *Rhabdocline* in the Southwest is not *Rhabdogloeum Pseudotsugae* and, in as much as its connection with *Rhabdocline* has not been conclusively established, should be regarded as a new *Rhabdogloeum,* which is described as follows:

Rhabdogloeum hypophyllum sp. nov.

Fruiting bodies hypophyllous, rarely epiphyllous, in reddish-brown conspicuous spots, scattered or confluent, often in parallel series on either side of the midrib, 130 to 500 μ wide by 35 to 150 μ high, average about 300 × 90 μ, raising the epidermis into elongate pustules 0.5 to 4 mm. long, at first covered, later erumpent. Conidia, hyaline, continuous, oblong, straight to slightly curved, often somewhat constricted near the middle, 6.7–11.1 × 2.2–3.7 μ, average 9.1 × 3 μ. Conidiophores slender, simple, continuous or septate, 10–56 × 0.9–2.8 μ, average 28.3 × 1.8 μ.

Acervuli hypophylli, rare epiphylli, dispersi vel confluentes, saepe in seriebus parallelibus dispositi, primum tecti et epidermidem in pustulis elongatis 0.5–4 mm. longis elevantes, dein erumpentes, 130–500 μ lati, 35–150 μ alti; conidia hyalina, continua, oblonga, recta vel subcurvata, saepe medio aliquantus constricta, 6.7–11.1 × 2.2–3.7 μ; conidiophora tenuia, simplicia, continua vel septata, 10–56 × 0.9–2.8 μ.[2]

Parasitic on needles of *Pseudotsugae taxifolia* (Poir.) Britt.: Arizona; New Mexico.

Type locality: Lincoln National Forest, near Cloudcroft, New Mexico.

[2] Latin description prepared by Miss Edith K. Cash, Associate Mycologist, Division of Mycology and Disease Survey, Bureau of Plant Industry, Soils, and Agricultural Engineering.

Specimens examined: The following specimens in the herbarium of the Division of Forest Pathology at Albuquerque, N. Mex , were examined:

Arizona—Crook National Forest: Hospital Flat, Graham Mountains, D. E. Ellis, May 13, 1939 (*89324*), June 21, 1939 (*89314*), May 9, 1940 (*89386*)

FIG. 2. A, camera-lucida sketch from free-hand section through a fruiting body undergoing transition from the imperfect to the perfect stage The remnants of the conidial stroma are shown on the right being pushed out by the developing asci B, photomicrograph of a section through a fruiting body undergoing transition from the imperfect to the perfect stage somewhat less advanced than in figure 2 A In this case the conidial layer is to the left and the ascogenous layer is just below, the asci being in a very early stage of development.

New Mexico.—Red River, R. K. Beattie and L. S. Gill, May 14, 1940 (*89391*). Lincoln National Forest: near Cloudcroft, L. S. Gill and D. E. Ellis, January 13, 1940 (*89371*), March 4, 1940 (*89374*), J. S. Hall, March 18, 1940 (*89376*), April 16, 1940 (*89383*), June 15, 1940 (*92530*), D. E. Ellis, May 23, 1940 (*89392*); James Canyon, L. S. Gill and J. S. Hall, April 4, 1940 (*89380*); Sacramento River, J. S. Hall, April 30, 1940 (*89384*); near Cloudcroft Nursery, L. S. Gill and G. G. Hahn, May 13, 1942 (*89639*), *type*.

A portion of the type collection is being deposited with the Mycological Collections of the Bureau of Plant Industry, Soils, and Agricultural Engineering.

It seems improbable, as Boyce (1, p. 171) has already pointed out, that *R. Pseudotsugae* is the imperfect stage of *Rhabdocline Pseudotsugae*, because the former is collected so seldom and has only been found in nature after the fruiting bodies of the latter are mature.

The work on this problem has been interrupted and the writers fully realize that additional critical studies will be necessary before definite conclusions can be drawn. However, it is felt that the above observations strongly suggest that *Rhabdogloeum hypophyllum*, which has been repeatedly found associated with *Rhabdocline Pseudotsugae* in the Southwest and successfully grown in artificial culture, is a stage in the life history of that organism.

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PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XXXIX. THE GENUS GODRONIA AND ITS ALLIES

Fred J. Seaver

(with 3 figures)

There seems to be much difference of opinion in the minds of mycologists as to the taxonomic status of the genus *Godronia* and its close allies. Far be it from the present writer to attempt to solve all the intricate nomenclatural problems involved but perhaps it is not out of place at this time for us to make our little contribution to the confusion already existing in an effort to bring together all the facts as viewed by a taxonomist.

The genus *Godronia* was founded by J. B. Mougeot (Consid. Gen. Veg. Vosges 355. 1845) and based on *G. Muhlenbeckii,* a species which seems not to be very well known. The characters of the genus however were well defined. Several years later the genus *Crumenula* was proposed by DeNotaris (Comm. Soc. Critt. Ital. 1: 363. 1863) based on *Peziza Urceolus* Alb. & Schw. In 1885 Karsten (Acta Fauna Fl. Fenn. 2: 143) made *Crumenula* a synonym of *Godronia.*

Rehm (Rab. Krypt.-Fl. 1^3: 237. 1896) retains both genera but transfers the type of *Crumenula* to *Godronia,* a procedure which would not be sanctioned under present day rules and practices. From that day on *Peziza Urceolus* has been regarded as the type of the genus *Godronia.* Those who have attempted to keep the two genera *Crumenula* and *Godronia* segregate them on the fact that the former has apothecia with a slightly tomentose or hairy exterior, while in the latter they are smooth, a character which would not appear to be of great importance. In 1863 DeNotaris also established the genus *Scleroderris* (Comm. Soc. Critt. Ital. 1: 383), based on *Peziza ribesia* Pers. At the present time mycologists are generally agreed that *Godronia* and *Scleroderris*

are synonymous. Nannfeldt goes a step farther (Nova Acta Soc. Sci. Upsal. IV. **8**: 282. 1932), combining *Godronia, Crumenula, Scleroderris* and *Durandia,* but treats *Scleroderris* as the valid name, probably because the type of the genus *Godronia* is not very well-known. Since the characters of the genus were well defined we believe the name *Godronia* should be retained. If Nannfeldt is correct in reducing *Durandia, Durandiella* Seaver should also be included since it was proposed to replace the name *Durandia* which is untenable. Groves (Mycologia **29**: 79. 1937) believes that *Durandiella* should be retained as distinct from *Scleroderris* or *Godronia.*

In 1930 a new genus was proposed by Zeller and Goodding (Phytopathology **20**: 561) for certain species which had previously been referred to *Scleroderris* but which they believed to be sufficiently distinct to constitute a separate genus. They proposed *Atropellis* with *Atropellis pinicola* Zeller and Goodding as the type species. The genus was to be disinguished from *Scleroderris* and *Godronia* by the non-septate spores—a character which is extremely variable in some groups—and the color of the apothecium and hymenium. But the type of *Atropellis* is very closely related and certainly congeneric with our *Crumenula pinicola* or, at least, what has passed as that species in the eastern United States. One of the characters of our so-called *Crumenula pinicola* is the purple color of the paraphyses when crushed and seen with transmitted light.

In order to get more information on the nature of the European *Crumenula,* in January 1937 a letter was addressed to J. A. Nannfeldt of Sweden requesting material of *Crumenula.* No material was available, but later Nannfeldt sent on loan slides of *Crumenula pinicola* (Rab.) Karst., and also *Crumenula sororia* Karst. We were much interested to note that both showed with transmitted light the same blue color which characterized the American material referred to *Crumenula pinicola.* While the spore characters were not altogether satisfactory in the prepared slides, we believe that our material is identical with *Crumenula pinicola* (Rab.) Karst. The same blue character has also been observed in *Atropellis pinicola* Zeller & Goodding. This and other characters would indicate that the two are congeneric.

In 1930 Groves (Mycologia 28: 451. 1936) discusses *Ascocalyx Abietis* Naumov, the conidal stage of which has long been known in America. The perfect stage was collected in northern Ontario. He concludes that *Ascocalyx Abietis* is probably congeneric with *Crumenula pinicola* (Rab.) Karst., but that it is not congeneric with *Crumenula Urceolus* (Alb. & Schw.) DeNotaris. He further believes that *Ascocalyx* is a valid genus and that species of *Crumenula* in the sense of Rehm should be transferred to *Ascocalyx*.

From this it will be seen that *Godronia* is a conglomerate genus made up of several units which have been brought together because they have certain characters in common but, eventually, it may be necessary to resolve it, or partially resolve it, into its component parts. For the time being, however, they may all be regarded as *Godronia*. It is our purpose here to list and discuss a number of species which are at the present time included in the genus.

The oldest described species at the present time included in the genus is *Peziza ribesia* Pers. (Tent. Disp. Fung. 35. 1797), later made the type of the genus *Scleroderris*, characterized by its much elongated slender ascospores. Bonorden (Handb. Mykol. 135. 1864) described the conidial stage of this fungus under the name *Fuckelia*. It consists of cylindrical or conical pycnidia divided into numerous chambers containing the pycnospores 4×6.5–$10\ \mu$. The pycnidia are at first closed but later burst open irregularly. Fuckel (Symb. Myc. 267. 1869) cites two conidial stages for this fungus, *Fuckelia Ribis* Bon. and *Mastomyces uberiformis* (Fries) Karst. (*Mastomyces Friesii* Mont.). Cash (Mycologia 26: 268. 1934) states that the former is the conidial stage of *Godronia Urceolus* (Alb. & Schw.) Karst. which often occurs on the same host which is doubtless responsible for the confusion.

The next earliest species at present considered in the genus is *Sphaeria fuliginosa* Pers. (Obs. Myc. 2: 68. 1799). A full account of this species was published by the writer (Mycologia 25: 55. 1933). So far as the writer is aware this species is known from only two collections in America, one by John Dearness in Ontario which Ellis described as a new species, *Lasiosphaeria striata,* and the other by the writer in collaboration with Ells-

worth Bethel which was again described as a new species, *Godronia Betheli* Seaver. It will be noted that twice this has been described as a sphaeriaceous fungus, due to the fact that the apothecia are for a long time closed and when young resemble large perithecia. This species occurs exclusively on willow. The report of the occurrence of this species, appearing in the Host Index of the Fungi of North America, under the name *Godronia Betheli,* on alder, was an error. The fungus collected and reported by C. H. Kauffman (Papers Mich. Acad. **1**: 109. 1921) is *Cyphella fasciculata,* a fungus which outwardly resembles the *Godronia* for which it was mistaken.

The pycnidia occur in congested groups accompanying the apothecia and resembling them in color. They are at first closed but seen to dehisce at maturity, forming miniature apothecial-like structures. The pynospores resemble the ascospores but are less than half as long.

The third species described which is now included in the genus is *Peziza Urceolus* Alb. & Schw. (Consp. Fung. 332. 1805), which occurs on twigs of various deciduous shrubs and trees. The pycnidial stage *Mastomyces* of this fungus has been discussed by Miss Cash (Mycologia **26**: 266. 1933), the pycnospores 3–4 × 26–30, 3-septa.

Following is the writer's conception of the genus:

GODRONIA Moug. Consid. Gen. Veg. Vosges 355. 1845.
Crumenula De-Not. Comm. Critt. Ital. **1**: 365. 1863.
Scleroderris (Fries) De-Not. Comm. Critt. Ital. **1**: 383. 1864.
Durandia Rehm, Ann. Myc. **11**: 166. 1913.
Ascocalyx Naumov, Bolesni Rast. **14**: 138. 1925.
Atropellis Zeller & Goodding, Phytopathology **20**: 561. 1930.
Durandiella Seaver, Mycologia **24**: 261. 1932.

Type species, *Godronia Muhlenbeckii* Moug. & Lév.

Mougeot describes the genus as having apothecia which are coriaceous or gelatinous like *Bulgaria,* and with the spores of a *Stictis.* The genus *Godronia* and the genus *Stictis* are strikingly similar and might easily be confused, notwithstanding the fact that they are placed in different orders.

The genus is characterized by the erumpent apothecia and the very much elongated or filiform spores which usually become 1-

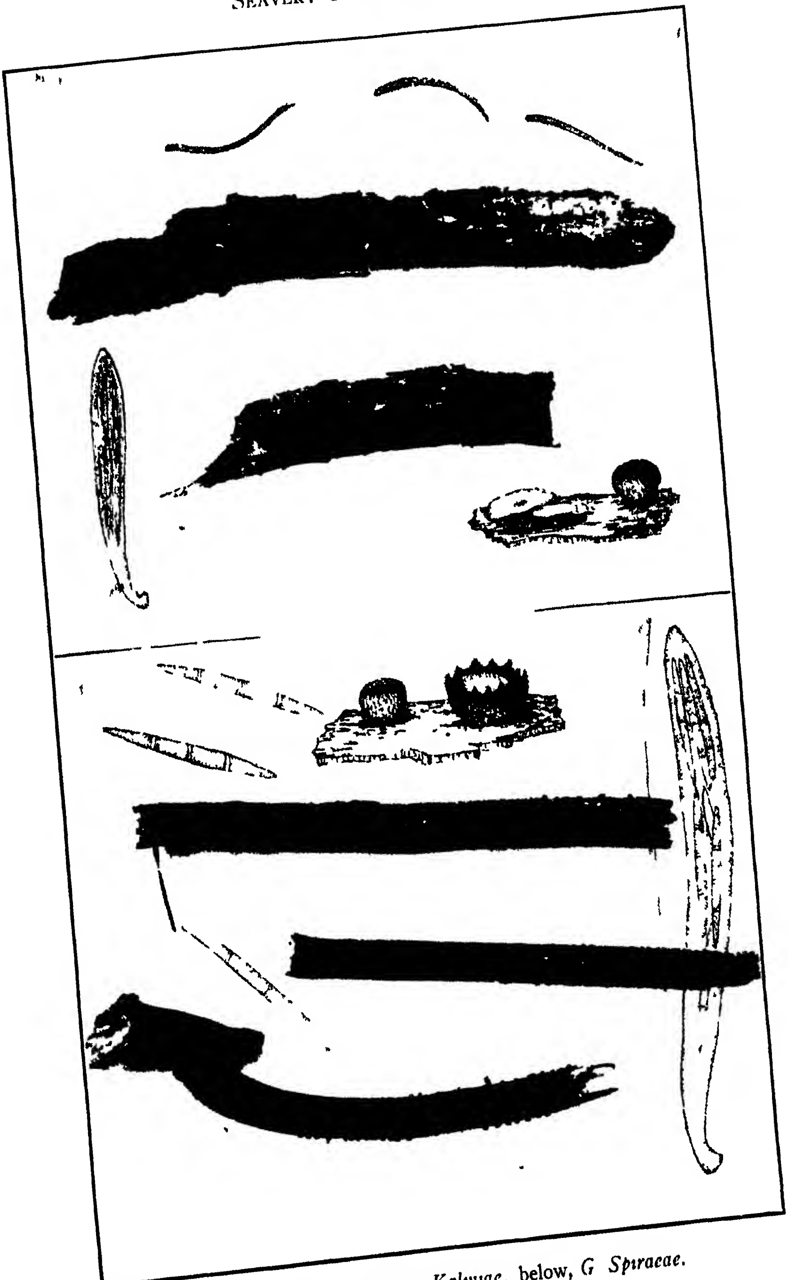

Fig 1. Above, *Godronia Kalmiae*, below, *G Spiraeae*.

to several-septate, although they may be for a long time without septa, as in other species of Cenangiaceae.

On deciduous woody plants.	
Spores relatively short, less than half the length of the ascus.	
On stems of *Ribes*.	
In congested masses; spores clavate.	
Spores becoming 3-septate.	
Spores 20–38 μ.	1. *G. Ribis.*
Spores 18–20 μ.	2. *G. lobata.*
Spores simple, in specimens studied.	3. *G. tumoricola.*
Occurring singly; spores fusoid.	4. *G. Davidsoni.*
Not on *Ribes*.	
Spores fusoid.	
Spores 11–17 μ long; on *Lantana*.	5. *G. Lantanae.*
Spores 20–24 μ long.	
Apothecia turbinate; hymenium concave.	6. *G. turbinata.*
Apothecia patellate; hymenium plane or nearly so.	7. *G. fusispora.*
Spores 25–40 μ long.	
Apothecia with a laciniate border on *Spiraea*; spores 3–4 × 25–35 μ.	8. *G. Spiraeae.*
Apothecia not laciniate on *Vitis*; spores 3–4 × 35–40 μ.	9. *G. viticola.*
Spores slender, rod-like; 1.5–2 × 10–12 μ.	10. *G. Lonicerae.*
Spores relatively long, more than half as long as the ascus.	
On stems of woody plants.	
Spores long-fusoid.	
Apothecia deeply concave; on *Salix*.	11. *G. fuliginosa.*
Apothecia slightly concave; on *Betula*.	12. *G. seriata.*
Spores filiform or vermiform.	
Spores short, 25–30 μ long; on *Kalmia*.	13. *G. Kalmiae.*
Spores 40–75 μ long.	
Spores slender, 1.5–2 μ thick.	
Apothecia cespitose, discoid.	14. *G. Nemopanthis.*
Apothecia scattered, urceolate.	15. *G. Urceolus.*
Spores 3–4 μ in diameter, nearly as long as the ascus.	
Apothecia scattered; on sage brush.	16. *G. montanensis.*
Apothecia in cespitose clusters.	
Spores 3 × 65–70 μ; on *Cephalanthus*.	17. *G. Cephalanthi.*
Spores 3–4 × 85–100 μ.	
On *Viburnum*.	18. *G. viburnicola.*
On *Fraxinus*.	19. *G. Fraxini.*
Spores 6 × 75 μ vermiform; on *Quercus*.	20. *G. tabacina.*

Spores very long, nearly as long as the ascus.	
On leaves of *Tetrazygia*, spores 250 µ long.	21. *G. parasitica.*
On branches of *Castanopsis.*	22. *G. Castanopsidis.*
On coniferous branches.	
Paraphyses blue with transmitted light.	
Spores 1–3-septate.	23. *G. pinicola.*
Spores simple or doubtfully septate.	
Spores 1.5–3.5 × 32–63 µ.	24. *G. Zelleri.*
Spores 5–6 × 15–22 µ.	25. *G. sororia.*
Paraphyses not blue.	
Hymenium light colored.	
Hymenium pink to brown; on *Picea* in Alaska.	26. *G. Treleasei.*
Hymenium pale yellow or whitish; on *Juniperus* in Jamaica.	27. *G. jamaicensis.*
Hymenium grayish to black; on *Abies.*	28. *G. Abietis.*

1. **Godronia Ribis** (Fries) comb. nov.

Peziza ribesia Pers. Tent. Disp. Fung. 35. 1797.
Cenangium Ribis Fries, Syst. Myc. **2**: 179. 1822.
Tympanis Ribis Wallr. Fl. Crypt. Ger. **2**: 430. 1833.
Crumenula Ribis Karst. Fungi Fenn. Exsicc. *929.* 1870.
Scleroderris ribesia Karst. Myc. Fenn. **1**: 215. 1871.

Apothecia erumpent in cespitose clusters, 1–3 mm. in diameter from a stromatic base, each cluster consisting of 4–12 apothecia, individual apothecia at first globose or subglobose, short stipitate gradually expanding and becoming shallow cup-shaped, with a notched or fimbriate margin, reaching a diameter of 1–2 mm., blackish-brown; hymenium concave, pale cinereous; asci clavate-cylindric, reaching a length of 90–100 µ and a diameter of 7–8 µ, 8-spored; spores much elongated, clavate, 3–4 × 20–38 µ, becoming 3-septate; paraphyses filiform, slightly enlarged above.

Pycnidia, *Fuckelia Ribis*, present; pycnospores elongate-clavate, 3–4 × 7–11 µ, usually containing two oil drops.

On branches of species of *Ribes.*

TYPE LOCALITY: Europe.

DISTRIBUTION: Toronto, Canada; also in Europe.

ILLUSTRATIONS: Boud. Ic. Myc. *pl. 563;* Ann. Sci. Nat. III. **20**: *pl. 16, f. 9–11;* Tul. Fung. Carp. **3**: *pl. 19, f. 1–9;* Rab. Krypt.-Fl. **1**^{3}: 200, *f. 1–2;* 201, *f. 6, 7;* E. & P. Nat. Pfl. **1**^{1}: 255, *f. 187.*

2. **Godronia lobata** (Cash) comb. nov.
Scleroderris lobata Cash, Mycologia **28**: 248. 1936.

Apothecia breaking through the bark usually in clusters of 2–4 or rarely single, subglobose to cupulate, opening by splitting into 4–6 lobes which fold over one another on drying, reaching 1 mm. in diameter and height, externally blackish-brown, smooth; hymenium concave, light olive-gray; asci cylindric, short-stipitate, rounded and slightly narrowed above, reaching a length of 90–115 μ and a diameter of 7–9 μ; spores 1-seriate below, 2-seriate above, clavate, usually 3-septate, 3–4 × 18–20 μ; paraphyses filiform, simple or branched near the tip, slightly enlarged above.

On twigs of *Ribes Menziesii.*

TYPE LOCALITY: Spruce Cove, Trinidad, California.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Mycologia **28**: 250, *f. 3.*

3. **Godronia tumoricola** (Cash) comb. nov.
Scleroderris tumoricola Cash, Mycologia **26**: 270. 1934.

Apothecia sessile, usually cespitose or rarely single, cup-shaped to nearly plane, triangular or irregularly contorted when dry, coriaceous, blackish-brown to black, .5–2 mm. in diameter; hymenium concave to plane, drab, drying nearly black; asci cylindric, narrowed above, reaching a length of 90–100 μ and a diameter of 5–8 μ, 8-spored; spores 2-seriate or irregularly 1-seriate, clavate with the acute end below, simple (later septate?), 1.5–2 × 10–15 μ; paraphyses filiform, hyaline simple or branched near the middle, enlarged above to 2 μ in diameter.

On swollen canker-like areas on twigs of *Ribes montigenum.*

TYPE LOCALITY: Mesa Lakes, Grand Mesa National Forest, Colorado.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Mycologia **26**: *pl. 32, f. 4.*

This species was placed in the genus *Scleroderris* on the supposition that the spores would finally become septate although no septa were apparent in the specimens studied. The spores in other Cenangiaceae often become tardily septate.

4. GODRONIA DAVIDSONI Cash, Mycologia **26**: 269. 1934.

Apothecia sessile or substipitate, single, depressed-globose to urceolate, not exceeding 1 mm. in diameter and height, dark col-

ored, greenish-olive, opening with a circular opening, with a fimbriate margin; hymenium concave, smoky-gray; asci cylindric gradually narrowed toward the base and above, 8-spored, reaching a length of 90–120 μ and a diameter of 5–7 μ; spores acicular-fusoid, parallel or slightly twisted in the ascus, becoming 3-septate, 2.5–3 × 33–45 μ; paraphyses filiform, simple, hyaline, gradually enlarged above, reaching a diameter of 2–2.5 μ, often curved at the tips.

On stems of *Ribes Wolfii, R. bracteosum* × *R. nigrum.*

TYPE LOCALITY: Near Mesa Lakes, Grand Mesa National Forest, Colorado.

DISTRIBUTION: Colorado and Alaska.

ILLUSTRATIONS: Mycologia **26**: 269, *f. A; pl. 32, f. 3.*

5. **Godronia Lantanae** (Cash) comb. nov.

Scleroderris Lantanae Cash, Mycologia **30**: 100. 1938.

Apothecia cespitose, sessile, cupulate to discoid, contorted by mutual pressure, reaching a diameter of 1–1.5 mm., furfuraceous, brown, the margin inrolled when dry, sometimes becoming hysteroid; hymenium concave to plane, brownish-black; asci clavate, rounded above, gradually narrowed toward the base, 8-spored, reaching a length of 50–55 μ and a diameter of 5 μ; spores 2-seriate, fusoid, straight or slightly curved, becoming 1-septate, hyaline to pale brownish, 1.5–2 × 11–17 μ; paraphyses simple, 2.5 μ in diameter at their apices.

On fallen branches of *Lantana camara.*

TYPE LOCALITY: Kaluaaha Valley, Molokai, Hawaii.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATION: Mycologia **30**: 99, *f. 4.*

6. GODRONIA TURBINATA (Schw.) Farlow, Mycologia **14**: 101. 1922.

Tympanis turbinata Schw. Trans. Am. Phil. Soc. II. **4**: 237. 1832.

Apothecia erumpent, turbinate, with the mouth strongly constricted, brownish-black, furfuraceous, reaching a diameter of 1 mm.; hymenium deeply concave, pallid; asci clavate, reaching a length of 110 μ and a diameter of 6–7 μ, apparently 8-spored; spores often indistinct, fusiform, about 2 × 20 μ, 3-septate.

On twigs of *Diervillea.*

TYPE LOCALITY: Bethlehem, Pennsylvania.

DISTRIBUTION: Pennsylvania and Maine.

EXSICCATI: Reliq. Farlow. *122.*

This description is based on material collected by Dr. R. Thaxter at Kittery Point, Maine. Material in the Schweinitz collection in Philadelphia is scant and uncertain.

7. **Godronia fusispora** (Ellis & Ev.) comb. nov.

Dermatea fusispora Ellis & Ev. Proc. Acad. Phila. **1893**: 148. 1893.

Apothecia scattered, occurring singly or occasionally 2 or 3 crowded together, externally subolivaceous, reaching a diameter of 1 mm.; hymenium plane or nearly so with a slightly elevated margin, reddish; asci clavate, 8-spored, reaching a length of 70–75 μ and a diameter of 6–7 μ; spores narrow fusoid, 2–3 × 20–24 μ; paraphyses filiform, slightly enlarged above, reaching a diameter of 2–3 μ.

On dead branches of *Betula* sp.

TYPE LOCALITY: Orono, Maine.

DISTRIBUTION: Known only from the type locality.

8. **Godronia Spiraeae** (Rehm) comb. nov.

Scleroderris Spiraeae Rehm in Rab. Krypt. Fl. 1^3: 1220. 1896.

Apothecia subsessilis, thickly gregarious, occurring singly or rarely with two or three crowded together, subglobose, with the mouth constricted (in dried specimens) and laciniate, dark brownish-black, often with a greenish tint, reaching a diameter of 1 mm.; hymenium concave, obscured when dry by the incurved margin, freely exposed when moist, light brown; asci cylindric-clavate, reaching a length of 80–85 μ and a diameter of 6–7 μ, 8-spored; spores fusoid, overlapping and subfasciculate, 3–4 × 25–35 μ, becoming 3-septate; paraphyses slender, slightly enlarged above (FIG. 1, lower).

On branches of *Spiraea salicifolia.*

TYPE LOCALITY: Hewitt's Pond, New York.

DISTRIBUTION: Known only from the type locality.

Described from material in the herbarium of The New York Botanical Garden, collected by C. H. Peck in July (the year not indicated).

9. GODRONIA VITICOLA (Schw.) Farlow; Thaxter, Mycologia **14**: 101. 1922.

Peziza viticola Schw. Schr. Nat. Ges. Leipzig **1**: 123. 1822.
Cenangium viticolum Sacc. Syll. Fung. **8**: 572. 1889.

Apothecia scattered or gregarious, scutellate to subdiscoid, black or blackish, soft and subgelatinous when moist, reaching a diameter of 15 mm.; asci clavate, tapering below into a slender stem-like base, reaching a length of 85 μ and a diameter of 12 μ, 8-spored; spores fusoid, 1–3-septate, 4 × 35–40 μ; paraphyses filiform.

On bark of living grape vine, *Vitis* sp.

TYPE LOCALITY: North Carolina.

DISTRIBUTION: North Carolina to New Jersey.

EXSICCATI: Ellis, N. Am. Fungi *1317*.

10. **Godronia Lonicerae** sp. nov.

Apothecia sessile or subsessile, attenuated below at first closed, externally dark colored, striated near the margin and clothed with poorly developed adpressed hairs, gradually expanding but with the margin constricted, .3 mm. diameter; hymenium dull but lighter than the outside of the apothecium; asci clavate, reaching a length of 40–45 μ and a diameter of 6–7 μ, 8-spored; spores slender rod-like 1.5–2 × 10–12 μ, containing several oil drops; paraphyses filiform, 1.5–2 μ in diameter, slightly enlarged above, hyaline.

Apotheciis sessilis vel subsessilis, extus striatis, sordidis vel subatris, subtomentosis, primo clausis demum expansis, ore constricto, .3 mm. diam.; hymenio sordido; ascis clavatis, 6–7 × 40–45 μ, 8-sporis; sporis elongatis, guttulatis, 1.5–2 ×10–12 μ; paraphysibus filiformibus, apice leniter incrassitis, 1.5–2 μ diam.

On branches of *Lonicera canadensis*.

Type collected by R. F. Cain, June 17, 1931 at Lake Temagami, Toronto, Canada.

11. **Godronia fuliginosa** (Pers.) comb. nov.

Sphaeria fuliginosa Pers. Obs. Myc. **2**: 68. 1799.

Cenangium difforme Fries; Moug. & Nest. Stirp. Crypt. 889. 1826.

Cenangium fuliginosum Fries, Elench. Fung. **2**: 23. 1828.

Tympanis difforme Pers.; Tul. Fung. Carp. **3**: 166. 1865.

Scleroderris fuliginosa Karst. Myc. Fenn. **1**: 216. 1871.

Lasiosphaeria striata Ellis & Ev. Proc. Acad. Sci. Phila. **1893**: 443. 1894.

Godronia Betheli Seaver, Mycologia **3**: 64. 1911.

Godronia striata Seaver, Mycologia **4**: 123. 1912.

Apothecia erumpent through the outer bark of the host, single or occurring in clusters, often so numerous as to form congested masses many cm. in extent and often almost entirely surrounding the branches on which they grow, the individual apothecia at first nearly globose, opening at the top so as to leave an irregular margin, at maturity about 1 mm. broad and the same in height, brownish and furfuraceous externally and longitudinally striated; hymenium whitish or bluish-white; asci clavate, reaching a length of 130 μ and a diameter of 7–8 μ, 8-spored; spores fasciculate in the ascus, subfiliform, tapering toward either end, sharp-pointed, 3–4 $\times$ 65–85 μ, becoming 7-septate at maturity and often slightly constricted at the septa, hyaline; paraphyses abundant, filiform.

Pycnidia often accompanying the apothecia, at first closed becoming shallow cup-shaped, usually black; pycnospores fusiform, straight or slightly curved, 3-septate, 3–4 $\times$ 28–30 μ.

On branches of *Salix*.

TYPE LOCALITY: Europe.

DISTRIBUTION: Ontario and Colorado; also in Europe.

ILLUSTRATIONS: Tul. Fung. Carp. **3**: *pl. 20, f. 1–4;* E. & P. Nat. Pfl. 1^1: 255, *f. 187, H–J;* Rab. Krypt.-Fl. 1^3: 201, *f. 3–7;* Mycologia **25**: *pl. 15,* upper figure.

This species was collected in abundance on willow at Tolland, Colorado, by the author in company with Ellsworth Bethel in 1910 and described as a new species, *Godronia Betheli.* Later study revealed the fact that *Lasiosphaeria striata* Ellis & Ev. is identical but owing to the fact that it had been placed in the Sphaeriales it had been overlooked. The young apothecia are strongly constricted which doubtless accounts for the fact that

Ellis placed it in that group. Recent study has revealed the fact that both Ellis and Everhart's species and the species of the writer are identical with *Cenangium fuliginosum* of Fries.

Specimens erroneously reported on *Alnus* by Kauffman (Papers Michigan Acad. **1**: 109. 1923) have been examined and proved to be *Cyphella fasciculata* (see herbarium).

12. **Godronia seriata** (Fries) comb. nov.

Cenangium seriatum Fries, Sys. Myc. **2**: 185. 1822.
Phacidium seriatum Fries, Elench. Fung. **2**: 131. 1828.
Triblidium seriatum Fries, Scleron Suec. *161*.
Dermatea seriata Tul. Fung. Carp. **3**: 160. 1865.
Gelatinosporium betulinum Peck, Ann. Rep. N. Y. State Mus. **25**: 84. 1873.

Apothecia occurring in elongated clumps 3–4 mm. long and about 2 mm. broad, closely compressed together and often slightly irregular from mutual pressure, entirely black, reaching a diameter of .5 mm.; hymenium slightly concave, bordered by a slightly upturned margin, black; asci clavate, reaching a length of 95–110 μ and a diameter of 10–12 μ, 8-spored; spores long, fusiform and usually slightly curved when free, reaching a length of 45–60 μ and a diameter of 2–3 μ, 3-septate; paraphyses slender, branched, hyaline or subhyaline.

The conidial stage accompanies the ascigerous and consists of a blackish stroma in which the pycnospores are produced; pycnospores fusiform strongly curved and 3-septate, reaching a length of 40–45 μ from tip to tip and a diameter of 2–3 μ.

On *Betula lutea* and *Betula fontanilis*.

TYPE LOCALITY: Europe.

DISTRIBUTION: New York to Pennsylvania and Colorado; also in Europe.

ILLUSTRATIONS: Mycologia **25**: *pl. 15, lower figure*.

EXSICCATI: Ellis, N. Am. Fungi *537–537b;* Fungi Columb. *853;* Shear, N. Y. Fungi *200*.

A fine collection of this species was obtained in Coal Creek Cañon, Colorado, by the writer and Paul F. Shope, in the summer of 1929 (No. *495*), and determined by Mr. W. W. Diehl as *Scleroderris seriata* (Fries) Rehm. This is the only perfect speci-

men of this in the herbarium of The New York Botanical Garden from America.

Material which seems to be a part of the type collection of *Gelatinosporium betulinum* Peck is found in our collection. A note apparently in the handwriting of C. H. Peck reads as follows: "Perhaps the same as *Sphaeronema seriatum* B. & C. possibly a condition of *Cenangium seriatum* Fr." This conclusion is undoubtedly correct since our material collected in Colorado shows both stages on the same stroma. The pycnospores agree very closely with those from Peck's type. No definite pycnidia could be detected.

13. **Godronia Kalmiae** (Rehm) comb. nov.
Gorgoniceps Kalmiae Rehm, Ann. Myc. **2**: 353. 1904.

Apothecia gregarious, erumpent, at first cyathoid, short-stipitate, finally becoming irregularly discoid, externally reddish-brown, reaching a diameter of 1 mm.; hymenium at first concave, becoming plane or convex, sordid-yellow; stem very short and stout, gradually expanding into the apothecium; asci cylindric-clavate, reaching a length of 40–50 μ and a diameter of 5–8 μ, 8-spored; spores filiform, straight or curved when freed from the ascus, no septa apparent, 1 × 25–30 μ; paraphyses filiform, slightly enlarged above, 1–1.5 μ in diameter (FIG. 1, upper).

On decaying branches of *Vaccinium corymbosum.*

TYPE LOCALITY: North America (exact locality not given).

DISTRIBUTION: Known only from the type locality.

EXSICCATI: Ellis, N. Am. Fungi *147* (as *Dermatea Kalmiae* Peck). This material which was incorrectly named by Ellis was made the type of a new species by Rehm.

14. GODRONIA NEMOPANTHIS (Peck) Sacc. Syll. Fung. **8**: 603. 1889.
Tympanis Nemopanthis Peck, Ann. Rep. N. Y. State Mus. **35**: 142. 1884.
Durandiella Nemopanthis Groves, Mycologia **29**: 75. 1937.

Apothecia occurring in cespitose clusters or occasionally single, sessile, slightly narrowed below, reaching a diameter of 1 mm. and a height of 1.5 mm., circular in form or becoming irregular from

mutual pressure, dull black, the consistency leathery to cartilaginous or horny when dry; hymenium at first concave, becoming plane or convex, black or olivaceous when moist; asci cylindric to clavate-cylindric, tapering below into a stem-like base, reaching a length of 80–125 μ and a diameter of 7–9 μ; spores hyaline, filiform, septate, attenuated at the ends, straight or variously curved, intertwined in the ascus, 1.5–2 × 50–85 μ; paraphyses hyaline, filiform, septate, branched, 1.5–2 in diameter, scarcely enlarged above, forming a yellowish hymenium.

On dead stems of *Nemopanthes canadensis* (*Nemopanthes mucronata*).

TYPE LOCALITY: Grafton, Rensselaer County, New York.

DISTRIBUTION: New York to Maine and Ontario.

ILLUSTRATIONS: Mycologia **29**: 76, *f. 3; 77, f. 4–9.*

15. GODRONIA URCEOLUS (Alb. & Schw.) Karst. Acta Soc. Fauna Fl. Fenn. **2**: 144. 1885.

Peziza Urceolus Alb. & Schw. Consp. Fung. 332. 1805.
Peziza globularis Pers. Myc. Eu. **1**: 326. 1822.
Cenangium Urceolus Fries, Syst. Myc. **2**: 182. 1822.
Sphaeria uberiformis Fries, Syst. Myc. **2**: 491. 1823.
Tympanis Urceolus Wallr. Fl. Crypt. **2**: 425. 1833.
Mastomyces Friesii Mont. Ann. Sci. Nat. III. **10**: 135. 1848.
Cenangium globulare Fries, Summa Veg. Scand. 364. 1849.
Crumenula Urceolus De-Not. Comm. Critt. Ital. **1**: 365. 1863.
? *Sphaeronema urceolata* Ellis, Bull. Torrey Club **6**: 107. 1876.
Godronia Cassandrae Peck, Ann. Rep. N. Y. State Mus. **39**: 50. 1886.
Cenangium urceolatum Ellis, Grevillea **6**: 9. 1887.
Cenangella urceolata Sacc. Syll. Fung. **8**: 591. 1889.

Apothecia scattered or rarely 5–7 closely crowded together, erumpent through the bark, usually with a short, thick stem, urceolate, reaching a diameter of .5–1.5 mm., externally brownish or brownish-black; hymenium grayish or pallid; stem very short and inconspicuous; asci clavate-cylindric, reaching a length of 90–125 μ and a diameter of 6–7 μ, 8-spored; spores filiform, many-septate, 1.5 × 50–75 μ; paraphyses filiform, 2 μ in diameter.

Reported on twigs of various kinds, *Alnus, Betula* and *Clethra.* American specimen on *Ribes* seems to agree.

TYPE LOCALITY: Europe.

DISTRIBUTION: Newfoundland to Michigan; also in Europe.

ILLUSTRATIONS: Alb. & Schw. Consp. Fung. *pl. 3, f. 4;* E. & P. Nat. Pfl. 1[1]: 234, *f. 178-G–J;* Rab. Krypt.-Fl. 1[3]: 217.

EXSICCATI: Ellis, N. Am. Fungi *990* (as *Cenangium urceolatum*).

Miss Daisy S. Hone in her Minnesota work (Minn. Bot. Studies **4**: 111. 1909) describes a variety *Godronia urceolata conferta* which was said to differ in the habitat on *Prunus pumila* as well as in the clustered habit of the apothecia and the slightly shorter spores.

Godronia Cassandrae described by Peck from material collected on *Cassandra calyculata* appears to be identical with the above.

Cenangium urceolatum Ellis is identical. The spores are described by Ellis as fusoid, 1-septate and 4 × 15 μ. These were apparently conidia or pycnospores. Such spores have been found in connection with other specimens. The ascospores in this species are typical.

16. **Godronia montanensis** sp. nov.

Apothecia scattered, erumpent, superficial, at first urceolate, later expanding and becoming subdiscoid, blackish and minutely verrucose, reaching a diameter of 1 mm.; hymenium concave or nearly plane, pale yellowish; asci cylindric, reaching a length of 175–185 μ and a diameter of 10–11 μ, probably 8-spored; spores filiform nearly as long as the ascus, about 3 μ in diameter, many-septate and apparently breaking up into segments in the ascus, the segments about as long as broad; paraphyses filiform, about 1.5 in diameter.

Apotheciis sparsis, erumpentibus, demum subsuperficialis, primo urceolatis demum expansis, planis vel leniter concavis, extus subatris, leniter granulosis, 1 mm. diam.; hymenio concavo vel plano, flavo; ascis cylindraceis, 10–11 × 175–185 μ, 8-sporis; sporis filiformibus, circiter asci longitudine, 3 μ diam., multiseptatis, disjunctis; paraphysibus filiformibus, 1.5 μ diam.

On sage brush.

TYPE LOCALITY: Sheridan, Montana.

DISTRIBUTION: Known only from the type locality.

This interesting species was found sparingly associated with *Dermatella montanensis* Ellis & Ev. and was probably overlooked by Ellis. The species differs from others examined in the spores becoming disjuncted in the ascus as well as in the size of the spores and asci.

17. **Godronia Cephalanthi** (Schw.) comb. nov.

Peziza Cephalanthi Schw. Schr. Nat. Gez. Leipzig **1**: 123. 1822.
Cenangium Cephalanthi Fries, Syst. Myc. **2**: 188. 1822.
Scleroderris Cephalanthi Farlow; Thaxter, Mycologia **14**: 102. 1922.

Apothecia erumpent, usually in congested clusters several mm. long, the individual apothecia scutellate with the margin, dark brownish-black, reaching a diameter of 2 mm.; hymenium concave, pale yellowish; asci cylindric, reaching a length of 65–70 μ and a diameter of 10–12 μ, 8-spored; spores filiform about 3×65–$70\ \mu$, hyaline, becoming 5–7-septate; paraphyses filiform slender (FIG. 2, lower).

On *Cephalanthus occidentalis.*

TYPE LOCALITY: South Carolina.

DISTRIBUTION: New York and New Hampshire to South Carolina.

EXSICCATI: Reliq. Farlow. *103.*

The description is drawn from material identified by C. H. Peck and W. G. Farlow. Specimens in the Schweinitz collection are immature and the spore characters therefore uncertain.

18. **Godronia viburnicola** sp. nov.

Apothecia erumpent in cespitose clusters of 2–10 each, the individual apothecia black, reaching a diameter of 1 mm., tapering below into a stem-like base; hymenium slightly concave or nearly plane, similar in color to the outside of the apothecium; asci cylindric-clavate, reaching a length of 110 μ and a diameter of 10–12 μ, 8-spored; spores filiform, 3–4×85–$100\ \mu$; paraphyses slender, branched, slightly enlarged above, and brownish.

Apotheciis erumpentibus, 2–10 caespitosis, atris, 1 mm. diam., turbinatis; hymenio leniter concavo vel subplano, atro; ascis cylindraceis vel clavatis, 10–$12 \times 110\ \mu$; 8-sporis; sporis filiformibus 3–4×85–$100\ \mu$; paraphysibus ramosia sursum incrassatis, pallide brunneis.

On *Viburnum cassinoides* and *Viburnum dentatum*.

TYPE LOCALITY: New Hampshire.

DISTRIBUTION: Known only from the type locality.

EXSICCATI: Reliq. Farlow. *154a, 154b.*

19. **Godronia Fraxini** (Schw.) comb. nov.

Peziza Fraxini Schw. Schr. Nat. Ges. Leipzig **1**: 123. 1822.
Tympanis Fraxini Fries, Syst. Myc. **2**: 174. 1822.
?Sphaeronema Fraxini Peck, Ann. Rep. N. Y. State Mus. **29**: 71. 1878.
?Sphaerographium Fraxini Sacc. Syll. Fung. **3**: 598. 1884.
Durandia Fraxini Groves, Mycologia **29**: 78. 1937.

Apothecia erumpent in clusters of 3–10 or rarely occurring singly, black or blackish, reaching a diameter of 1 mm., circular or irregular from mutual pressure; hymenium plane or nearly so, similar in color to the outside of the apothecium; asci clavate, reaching a length of 120–150 μ and a diameter of 10–12 μ, 8-spored; spores filiform, attenuated at either end, septate, 2.5–3 $\times$ 50–90 μ; accompanied by minute spore-like bodies; paraphyses filiform.

The apothecia often accompanied with *Sphaerographium Fraxini* which appears to be its conidal stage.

On branches of *Fraxinus americana*.

TYPE LOCALITY: North Carolina.

DISTRIBUTION: North Carolina to Massachusetts, Ontario and Ohio.

EXSICCATI: Barth. Fungi Columb. *3885;* Rehm, Ascom. *2027;* Reliq. Farlow. *155a-b.*

20. **Godronia tabacina** (Cooke) comb. nov.

Dermatea tabacina Cooke, Bull. Buffalo Acad. Nat. Sci. **3**: 24. 1877.

Apothecia erumpent, short-stipitate, usually in cespitose clusters or occurring singly, at first subglobose, becoming cup-shaped, externally bay-brown, slightly furfuraceous, reaching a diameter of .5 mm., when dry laterally compressed and decidedly hysteriiform; hymenium concave or nearly plane, paler than the outside of the apothecium, reddish-brown; asci clavate, reaching a length of

105 μ and a diameter of 18 μ, 8-spored; spores elongated, vermiform often attenuated at the ends, parallel with the ascus or twisted around, when free often indented like a rope about 6 $\times$ 75 μ; paraphyses thick clavate, reaching a diameter of 5 μ, brownish.

On branches of *Quercus*, especially *Quercus alba* and *Quercus coccinea.*

TYPE LOCALITY: New Jersey.

DISTRIBUTION: New Jersey.

EXSICCATI: Ellis, N. Am. Fungi *146;* Rehm, Ascom. *359;* Thümen, Myc. Univ. *1560.*

21. GODRONIA PARASITICA Seaver, Mycologia **24**: 354. 1932.

Apothecia scattered on the underside of the living leaf, especially along the midrib, erumpent, at first globose, becoming expanded but with the mouth constricted, black, reaching a diameter of .3–.5 mm.; hymenium dingy, more or less concealed; asci clavate, reaching a length of 250–300 μ and a diameter of 27 μ; spores fiiliform, nearly as long as the ascus and about 4 μ thick, many-septate, the number of the septa difficult to determine but more than 50 have been counted, reaching a length of 25, paraphyses slender and rather freely branched.

On leaves of *Tetrazygia longicollis.*

TYPE LOCALITY: Marmelade, Republic of Haiti.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Mycologia **24**: *pl. 9.*

This is described from material collected by Mr. George V. Nash, August 25, 1903 (Nash *793*). The species is distinguished by its huge asci and spores.

22. **Godronia Castanopsidis** sp. nov.

Apothecia thickly gregarious, erumpent through the bark, sessile, usually occurring singly; irregularly rounded, externally blackish, reaching a diameter of 2–3 mm.; hymenium plane with a dark elevated margin, pale yellowish or nearly white; asci subcylindric, tapering below into a stem-like base, attenuated above, reaching a length of 300 μ and a diameter of 16–18 μ, 8-spored; spores filiform, nearly as long as the ascus, hyaline, septate, 2 μ in diameter; paraphyses filiform, branched, pale yellowish, scarcely enlarged above, 2–3 μ in diameter.

Apotheciis gregariis, erumpentibus sessilis, simplex; suborbicularis extus atris, 2–3 μ diam.; hymenio plano margine elevato, dilute flavo vel subalbo; ascis subcylindraceis apice attenuatis, stipitatis, 16–18 × 300 μ, 8-sporis; sporis filiformibus 250 μ long 2 μ diam.; hyalinis septatis; paraphysibus filiformibus, ramosis.

On dead branches of *Castanopsis chrysophylla.*

TYPE LOCALITY: Mount Shasta, California.

DISTRIBUTION: Known only from the type locality.

23. GODRONIA PINICOLA (Reb.) Karst. Acta Soc. Fauna Fl. Fenn. **2**: 144. 1885.

Peziza pinicola Reb. Fl. Neom. 385. 1804.

Peziza pinicola solitaria Fries, Syst. Myc. **2**: 113. 1822.

Heterosphaeria pinicola Fries, Summa Veg. Scand. 365. 1849.

Crumenula pinicola Karst. Myc. Fenn. **1**: 210. 1871.

Apothecia erumpent-superficial, at first rounded, expanding and becoming shallow cup-shaped to scutellate black with a purplish tinge (purple by transmitted light) furfuraceous or slightly hairy, reaching a diameter of 2–3 mm., sessile or short stipitate; hymenium concave or nearly plane, similar in color to the outside of the apothecium; asci clavate, reaching a length of 120 μ and a diameter of 12 μ, 8-spored; spores in a fascicle near the end of the ascus or irregularly disposed, fusiform, hyaline, 3–4 × 24–36 μ, becoming 1–3-septate; paraphyses slender, branched and forming a purplish epithecium (FIG. 3, upper).

On living branches of *Pinus rigida, P. pungens* and *P. resinosa.*

TYPE LOCALITY: Europe.

DISTRIBUTION: New Hampshire to Pennsylvania; also in Europe.

ILLUSTRATIONS: Not. Fauna Fl. Fenn. **10**: *pl. 2, f. e;* Mycologia **18**: 182, *f. 1, B–C;* Rab. Krypt.-Fl. **1**^{3}: 217, *f. 1–5;* E. & P. Nat. Pfl. **1**^{1}: 234, *f. 178, A–C.*

This was listed by L. O. Overholts as a *Crumenula* and possibly *Crumenula pinicola* (Reb.) Karst. in Mycologia **18**: 181. It agrees reasonably well with the descriptions of that species except for the purplish color which was not mentioned by Karsten. It is, however, thought best to refer American specimens to that species.

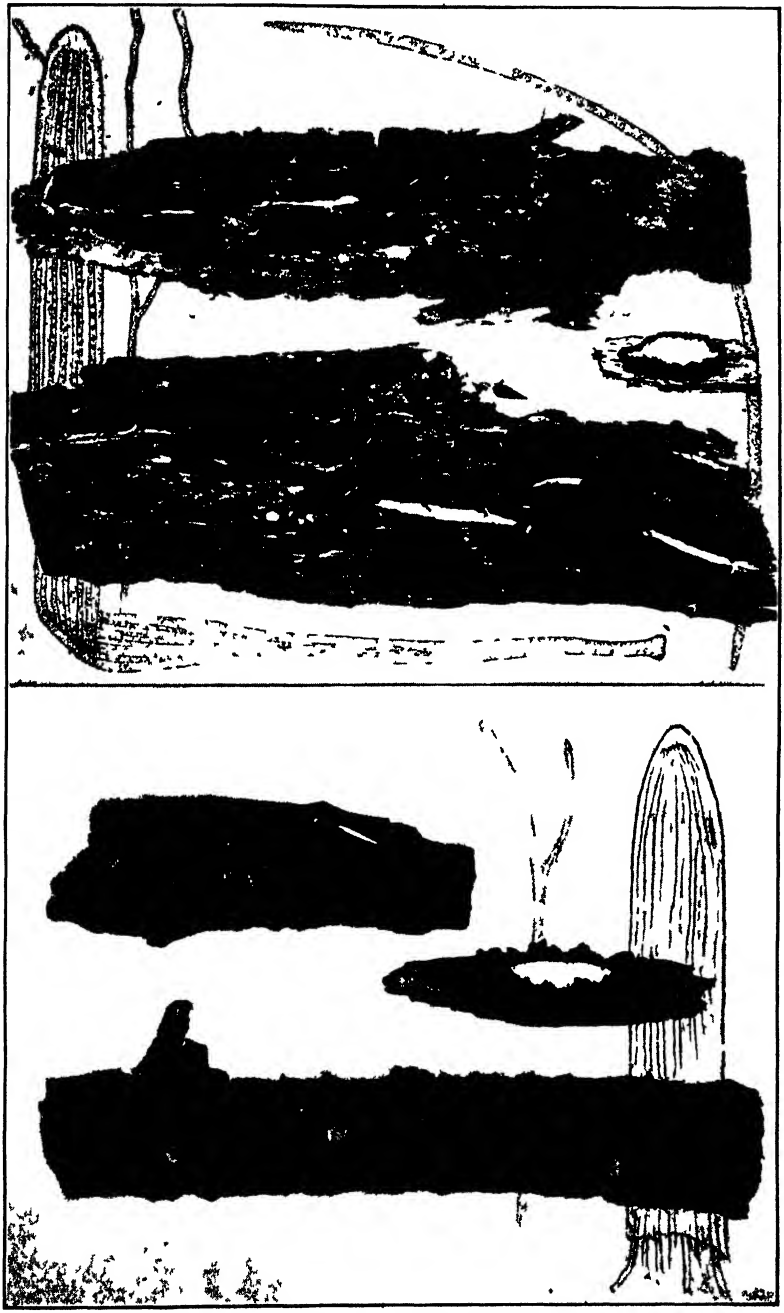

FIG. 2. Above, *Godronia jamaicensis*, below, *G. Cephalanthi*.

24. **Godronia Zelleri** nom. nov.

Atropellis pinicola Zeller & Goodding, Phytopathology **20**: 563. 1930. Not *Godronia pinicola* (Reb.) Karst. 1882.

Apothecia solitary or gregarious, erumpent from outer cortical layers of bark, sessile or on very short central stalk, 2–4 mm. in diameter, at first closed, opening by stellate or irregular clefts, leaving rather fimbriate margins, expanding discoid, usually rolling up from two sides when drying, externally pruinose, black to fuscous-black; hymenium pruinose, black; asci clavate, hyaline, staining brown with iodine, 8-spored, 74–178 × 8–13 μ (average 100 × 11 μ); spores filiform to acicular-clavate, hyaline continuous, guttulate, 32–63 × 1.5–3.5 μ (average 40 × 2 μ); paraphyses hyaline, hair-like, flexuous, exceeding the length of the asci by 32–38 μ, tips slender, agglutinated, forming a dense epithecium with rosy and purplish tints in section.

Imperfect stage usually associated with *A. pinicola:*

Fuckelia: Stromata erumpent, sometimes scattered, mostly gregarious, black, pulvinulate, sessile to short-stipitate, 0.8–1.2 mm. in diameter, containing 16–35 locules (pycnidia); conidiophores from entire inner surface of pycnidia, hair-like, simple, and branched; conidia hyaline, continuous, narrowly ellipsoid to bacillar, 8–11 × 1.7–3 μ.

On living branches and trunks of *Pinus monticola* and *P. contorta.*

TYPE LOCALITY: Oregon.

DISTRIBUTION: Oregon to Montana and British Columbia.

ILLUSTRATIONS: Phytopathology **20**: *pl. 1, f. G–M.*

25. GODRONIA SORORIA Karst. Acta Soc. Fauna Fl. Fenn. **2**: 145. 1885.

Crumenula sororia Karst. Myc. Fenn. **1**: 211. 1871.

? Cenangium piniphilum Weir, Phytopathology **11**: 295. 1921.

Apothecia erumpent in congested masses 1 cm. or more in diameter, the individual apothecia black or with a purplish tinge (decidedly purple when teased out), irregularly cup-shaped, closing when dry and often irregularly hysteriform, externally furfuraceous; reaching a diameter of 2–4 mm.; hymenium concave, similar in color to the outside of the apothecium; asci clavate, tapering very gradually into a long stem-like base, reaching a length of 135 μ and a diameter of 12 μ, 8-spored; spores irregularly 2-seriate above, fusoid, granular within, often slightly con-

stricted near the center and appearing pseudoseptate, 5–6 × 15–22 μ; paraphyses very slender, branched above and forming a purplish epithecium (FIG. 3, lower).

Forming cankers on trunks of *Pinus ponderosa*.

TYPE LOCALITY: Europe.

DISTRIBUTION: Idaho; also in Europe.

ILLUSTRATIONS: Phytopathology **11**: 294, *f. 1*; 295, *f. 2*.

The only American material seen was collected in Idaho by J. R. Weir (*15532*) who writes: "Forming cankers on 16-year old pine, causing a black deposit to form." As pointed out by Karsten that species is similar to *G. pinicola* so far as apothecial characters are concerned. The specific name selected by Karsten doubtless indicates that it is a sister species to that one which was listed in the same paper. Both have the blue character with transmitted light which, however, was not mentioned by Karsten. Examination of authentic material of both species shows it to be present. The spores in this species are shorter and broader than in that one. It also has a black subiculum not noted in *G. pinicola.*

26. **Godronia Treleasei** (Sacc.) comb. nov.

Scleroderris Treleasei Sacc. Harriman Alaska Exp. **5**: 24. 1904.

Atropellis Treleasei Zeller & Goodding, Phytopathology **20**: 562. 1930.

Apothecia solitary, or gregarious, at first erumpent then entirely superficial, mostly sessile, at first pitcher-shaped, closed then scutellate, laciniately dehiscent, 2.5–4 mm. in diameter, expanding to 3–5 mm. when moistened; outside and margins torn, dusky purplish-gray (Ridgway), carbonaceous, rugose; hymenium flatly-concave to convexly expanded, waxy, "pinkish cinnamon to Sayal brown" (Ridgway); asci clavate with obtusely-acute apices, narrowly and long stipitate, 100–178 × 8–14 μ (average 100 μ without stipe, 167 μ with stipe), 8-spored; spores fasciculate in upper part of ascus, mostly filiform, often somewhat clavate, hyaline, continuous, 2–2.5 × 42–60 μ; paraphyses filiform, with simple or incurved furcate tips which very slightly exceed tips of asci, hyaline.

On bark of *Picea sitchensis*.

TYPE LOCALITY: Alaska.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Harriman Alaska Exp. **5**: *pl. 3, f. 7 a–g;* Phytopathology **20**: *pl. 1, f. A–E.*

27. **Godronia jamaicensis** sp. nov.

Apothecia scattered, erumpent through the outer bark, finally appearing quite superficial, sessile, becoming expanded and scutellate with a wavy margin, externally brownish-black and verrucose or wrinkled, reaching a diameter of 2 mm.; hymenium plane or slightly concave, surrounded by the upturned, blackish margin, pale yellowish or whitish; asci clavate, 8-spored, reaching a length of 175 µ and a diameter of 10–12 µ, 8-spored; spores filiform, nearly as long as the ascus, 1.5–2 µ in diameter, no septa apparent; paraphyses filiform, freely branched (FIG. 2, upper).

Apotheciis sparsis, erumpentibus, demum superficialis, sessilis demum planis, margine elevato, undulato, extus brunneo-atris, verrucosis vel corrugatis, 2 mm. diam.; hymenio plano vel leniter concavo, pallide flavo; ascis clavatis, 8-sporis, 10–12 × 175 µ; sporis filiformibus circiter asci longitudine, 1.5–2 mm. diam.; paraphysibus filiformibus, ramosis.

On bark of *Juniperus.*

TYPE LOCALITY: Cincohona, Jamaica, altitude 4500–5400 feet.

DISTRIBUTION: Known only from the type locality.

A liberal quantity of this material was collected by W. A. Murrill in 1908–1909, No. *495.* The host species was not named but since only one species of *Juniperus* occurs in Jamaica it must have been that *Juniperus lucayana.*

28. **Godronia Abietis** (Naumov.) comb. nov.

Fusisporium Bernice Berk. & Curt. Grevillea **3**: 147. 1875.
Cenangium pithyum Berk. & Curt. Grevillea **4**: 4. 1875.
Scleroderris pithya Sacc. Syll. Fung. **8**: 596. 1889.
Bothrodiscus pinicola Shear, Bull. Torrey Club **34**: 312. 1907.
Pycnocalyx Abietis Naumov, Bull. Soc. Oural. Sci. Nat. Trud. Bur Mykol. **35**: 34. 1915.
Ascocalyx Abietis Naumov, Bolesni Rast. **14**: 138. 1925.

Apothecia erumpent, usually in clusters of 3–6 arising from a rounded, black, basal stroma, circular or slightly wavy in outline, narrowed below, .3–1 mm. in diameter, dull black externally,

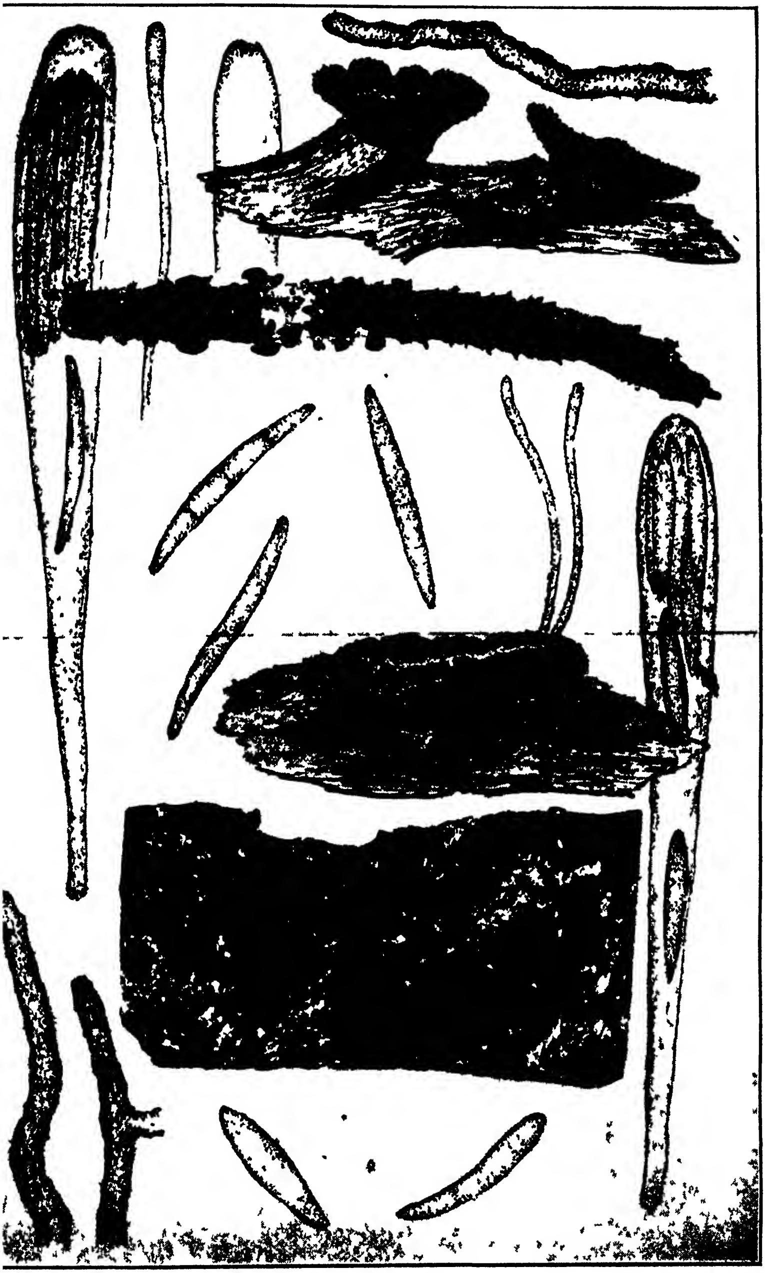

FIG 3 Above, *Godronia pinicola*, below, *G. sororia*

leathery to horny, becoming softer when moist; hymenium concave, becoming plane, smooth, gray to blackish, the margin infolded when dry; asci cylindric-clavate, short-stemmed, 8-spored, 9–11 × 65–100 μ; spores hyaline ellipsoid to subclavate, irregularly 2-seriate, simple becoming 1–3-septate, 4–5 × 14–22 μ; paraphyses hyaline, filiform, branched, 1.5–2 μ in diameter, scarcely enlarged above.

Pycnidia often arising from the stroma, at first almost globose, opening and becoming cup-shaped, reaching 2 mm. in diameter; pycnidial cavities immersed in the disc, ovoid, about 25–75 × 75–100 μ; conidiophores hyaline, tapering above, 8–12 × 1.5–2.5 μ; conidia hyaline, elongated to subfiliform, straight or curved, simple, becoming 1–5-septate, 3–5 × 16–24 μ.

TYPE LOCALITY: Europe.

DISTRIBUTION: New Hampshire to Michigan and North Carolina; also in Europe.

ILLUSTRATIONS: Mycologia **28**: 452, *f. 1;* 454, *f. 2;* 457, *f. 3–6.*

The above descriptions are based largely on Groves' records (Mycologia **28**: 451–462. 1936.) As pointed out by him, *Cenangium pithyum* Berk. & Curt. was based on the conidial stage.

DOUBTFUL AND EXCLUDED SPECIES

Godronia rugosa Ellis & Ev. Jour. Myc. **8**: 70. 1902. This species was described by Ellis from material collected at Tuskegee, Alabama, August, 1900 (G. W. Carver *479*). The spores are described as fusoid, arcuate, 45–55 × 3–3.5 μ. Examination of the Ellis material showed such spores but no trace of asci. It is probably not an ascomycete.

Godronia Juniperi Rostrup, Medd. Groenl. **3**: 611. 1891. Apothecia scattered, sessile, hard, black reaching a diameter of 1–2 mm.; asci fusoid-clavate, reaching a length of 75–85 μ and a diameter of 7–8 μ; spores filiform, 2 × 35–40 μ; paraphyses filiform. On wood of *Juniperus*. Known only from the type locality in Greenland.

Godronia rhabdospora (Berk. & Curt.) Sacc. Syll. Fung. **8**: 602. 1889. *Tympanis rhabdospora* Berk. & Curt. Grevillea **4**: 3. 1875. Spores said to be filiform. Reported on *Acer* from New England. No material seen.

EXPLANATION OF FIGURES

FIG. 1. Upper, *Godronia Kalmiae,* photograph of two pieces of wood with apothecia enlarged about one-half, also enlarged drawing of several apothecia, an ascus with spores and three spores freed from the ascus. Lower, *Godronia Spiraeae,* photograph of three twigs with apothecia, slightly enlarged, also drawings of two apothecia much enlarged, ascus with spores and paraphysis, also three spores freed from the ascus.

FIG. 2. Upper, *Godronia jamaicensis,* photograph of two pieces of wood with apothecia, about natural size, with drawing of one apothecium much enlarged, also ascus with spores and paraphysis, and one spore freed from the ascus. Lower, *Godronia Cephalanthi,* photograph of two fragments of wood with apothecia, enlarged about one-half, also enlarged drawing of one apothecium and portion of ascus with spores.

FIG. 3. Upper, *Godronia pinicola,* photograph of a piece of branch with apothecia about natural size, also drawing of apothecia much enlarged, ascus with spores and paraphysis, portion of empty ascus, three loose spores, and hairs from outside of apothecium. Lower, *Godronia sororia,* photograph of wood with apothecia, about natural size, also ascus with spores and paraphysis, two loose spores, and hairs from outside of apothecium.

SOME REMARKS ON MYCOGENETIC TERMINOLOGY

B. O. Dodge

The presidential address (Biological Section, Royal Society of Canada) "Life cycles and phylogeny in the fungi" by Professor H. S. Jackson (**1944**) will prove profitable reading, especially for botanists who are called upon to teach the more mature students in university courses. His work in the past has fitted him well to discuss the origin of the rusts and other Basidiomycetes. It is characteristic of him to assure us that his opinions are subject to revision in the event that new knowledge warrants a reconsideration. I have myself written many pages upholding the idea that in the fungi ascogonia and oogonia with their trichogynous outgrowths are female, and that antheridia, spermogonia and spermatia are male. Since these are morphological structures concerned with reproduction, we are justified in using them along with other features to mark the course taken by certain fungi in their evolution. The same can be said for pages in the support of the theory of the origin of the Ascomycetes and Uredinales from the Florideae. It is, therefore, gratifying to see how well we agree on the subjects he discusses. It may be well to point out, however, where we do not always quite agree with his statements or with the way he uses certain terms. I have, at one time or another, erred in the use of the same terms and upheld certain views which no longer seem tenable. I am, nevertheless, encouraged to make a few remarks relative to terminology in view of Professor Jackson's assurance that new knowledge always warrants a reconsideration.

"SEXUALITY IN THE FUNGI"

Under the above heading Jackson says that sexuality in the fungi has, both in the past and in the present, often been misunderstood and misinterpreted. To this we all agree. We do not all quite agree, however, when he says, "Though the correct inter-

pretation has often been properly stated. . . ." It is an open question whether Blakeslee's implication that the +/− relation in the Mucoraceae is to be looked upon as a female/male relationship.[1] Differentiation of ascogonial and antheridial structures is certainly advantageous, or even essential, in some species, in bringing about sexual reproduction. Certain botanists would insist that without such morphological differentiations there can be no sexual reproduction. We are glad to see that our author does not support such a view. He frequently refers to the two nuclei that fuse in the teliospore, ascus and basidium as sex nuclei, or direct descendants of sex nuclei. This, seemingly without regard as to where they originally came from; that is, whether or not male or female structures are involved in the process. I used to deny that the Christman cell fusions in the rusts are sex fusions, and also that there is ever sexual reproduction in the mushrooms because no male or female structures are developed. I now take a broader view. The essential thing in sexual reproduction is the fusion of two nuclei. Compared to this how insignificant are those structures which, while often advantageous, are often dispensable. In *Neurospora*, for example, there are all sorts of ways and devices for insuring that two genetically different nuclei finally come together to fuse in the young ascus. Heterothallism in the form of +/− relations is, as Jackson holds, an efficient provision for hybridization. Or, as I once said (**1936a**), "The important thing for purposes of evolution would be that +/− races have a genetic

[1] This +/− versus female/male relation has been rather well analyzed and evaluated by Moewus in a number of papers. (See Moewus, 1933 and 1938, for references.) In 1933 he looked upon the formation of zygotes in *Chlamydomonas eugametos* as the result of a +/− relation between two gametes which are genotypically different but phenotypically alike. He postulated sex stuffs indicating that zygote formation here constitutes sexual reproduction. About 1938, after he had found that his + races copulated with the smaller gametes of *C. Braunii* and the − races with the larger gametes, he discarded the +/− symbols and substituted ♀ and ♂ symbols. Moewus' papers should not be overlooked in our discussion of sex in the fungi even though we may not always agree with his philosophy. It would not be surprising to find that comparable sex stuffs are formed by races of many fungi when they are operating in this +/− relation. In any event why continue to magnify out of all proportion phenotypic sex differentiations when +/− relations are so important.

differentiation. It is also important not to confuse +/− genetic differences in heterothallic species with phenotypic cell differentiation in case of hermaphroditic species." While I do not exactly like those symbols, no one seems to have improved on them as a means of avoiding positive commitments one way or another.

In a number of Ascomycetes this relation is governed by a simple pair of factors which some of us designate as *A* and *a* without any thought of dominance. Their effectiveness in breeding work is often badly interfered with by incompatibility or sterility factors. For example, certain heterocaryotic races of *N. tetrasperma* and *Gelasinospora* types (although both *A* and *a* factors are present in the component nuclei) are self-sterile or self-incompatible because of interfering factors. Separate out or isolate the individual component races, *A* and *a*, mate them against suitable tester races, *a* and *A* respectively, and fertile ascocarps are forthcoming. (See also Dodge, 1935, p. 435.)

Jackson gives us three illustrations of "proper interpretation" of sex in the fungi. (1) He says that, because of misinterpretation, papers are being published in which the authors use the expression "thalli of opposite sex." What a grand opportunity was by-passed at this point. This was a good place to give us not only the correct expression for "thalli of opposite sex" but also the correct interpretation of sex, sex nuclei, and sexuality in the fungi. Instead, he says of the expression "thalli of opposite sex," ". . . it is abundantly evident that the species they are dealing with is properly to be interpreted as bisexual (hermaphroditic) self-sterile and interfertile." One may wonder just how a *species* can be self-sterile.

(2) Discussing *Puccinia graminis,* he says, "The two haploid thalli developed from + and − basidiospores are not of 'different sex,' but are properly to be interpreted as bisexual (sexually homothallic), hermaphroditic, intersterile and cross fertile." This means nothing in the way it is worded, and neither "interpretation" clarifies the point raised.[2] What should these erring authors have

[2] Prof. Paul Weiss (1945), in a number of Science which has just come to hand, has something to say apropos of our use of terms. "The creation of new terms or symbols, even if only for temporary use to designate complex phenomena or situations, which otherwise would have to be circumscribed

said? I have suggested as substitutes "thalli of opposite sex-reaction," "thalli of opposite mating types," or just plain "two + and − thalli." These expressions mislead no one. Our breeding work proves that "two thalli of opposite sex-reaction" can be, in certain cases, self-sterile, intersterile or cross-incompatible.

(3) Turning to homothallism, our author says, "The term has also unfortunately been applied in connection with certain Ascomycetes (*Neurospora, Pleurage, Gelasinospora*) which have four spores in an ascus. . . ." "Single nucleated isolates do not fruit. These forms are then basically heterothallic-hermaphroditic, self-sterile and interfertile." He omits here the first word "bisexual" with which he headed the interpretations in the two preceding illustrations. He characterizes *Gelasinospora* also as hermaphroditic when all its races are strictly "female" morphologically. No spermatia occur. Nevertheless (and this is what counts) normally the mycelium is heterocaryotic. Those who support the theory of relative sexuality could, of course, say that since all organisms, simple or complex, haploid or diploid, plant or animal, are potentially bisexual, *Gelasinospora* is potentially male even though it is actually only female. It is, therefore, bisexual (hermaphroditic). Such an argument would seem to be merely subterfuge.

Component races of *Gelasinospora* are of two sorts; these are races of opposite sex-reaction and they can be isolated very readily. Probably the two "female" races, the one + and the other − or of opposite mating type, will be found to synthesize sex stuffs, one kind female and the other kind male.

According to Blakeslee's original definition it was proper to characterize *N. tetrasperma* as homothallic, but when my cytological studies (**1927**, p. 294) proved that the small ascospores had only a single nucleus each at their origin, I looked upon races derived from them as "pseudoheterothallic." The expression

at each mention by long-winded phrases, should be encouraged." This reminds me of my own attitude when (**1932**) I said, "Is it necessary to explain again that I always use the terms 'sex' and 'opposite sex' simply for convenience until some one tells us just what it is that sets off the mechanism which regulates perithecium formation?" The same plea for the appropriate definition of sex or a term to be used instead of "opposite sex" has been repeated many times in print without response.

"facultatively heterothallic" was used in later papers (**1935**, **1936**, **1936a**) to characterize the four-spored species of *Neurospora*, *Gelasinospora* and *Pleurage*. I do not recall who originally proposed this expression. There is still a chance for a better term, one which distinguishes without a lot of explanation the four-spored types from the eight-spored types. To say that both are basically heterothallic misses the crucial differences when we are comparing *Neurospora tetrasperma* with *N. sitophila*. According to Jackson's own strictures (See his interpretation No. 2 above), *N. tetrasperma* would be doubly *homothallic* because he characterizes *Puccinia graminis* as sexually *homothallic*.

If one will study the cytological pictures (Dodge, **1942**, *fig. 1, 2*) one must be convinced that there is something besides mere compatibility relations that draws two nuclei of opposite mating types together so beautifully at the 4-nucleate stage of the ascus. This "sex" reaction, or attraction, no doubt due to sex stuffs, has the effect of providing heterocaryotic ascospores. If sex hormones ever operate in the fungi they are operating here in the ascus and in a +/− relation, where the "survival value" of Lindegren (**1933**) is reversed. Survival here is insured by providing compatible, and not incompatible nuclei for the heterocaryon. Self-sterile heterocaryotic races of *N. tetrasperma* are more often of our own making through hybridizing mutant races. By proper manipulation one can obtain a rather complicated heterocaryon through nuclear migration. The resultant effect on vegetative growth characters may appear superficially to be one of dominance, even when the genes concerned are not allelic. If we are in the mood for change we can, of course, alter our concept of dominance to cover resultant effects of a conglomeration of genes in a built-up heterocaryotic haploid. The dominant-recessive relation even in the diploid ascus is not a very stable one, so we need not worry too much about dominance in haploids. The lethals *I* and *E* (Dodge, **1934**, **1939**) are truly dominant but only so when they actually cause ascus abortion in asci which are heterozygous *Ii* or *Ee*. It has often been cited, as an illustration of dominance, the situation which arises when one crosses 4-spored *N. tetrasperma* with 8-spored *N. sitophila* and finds that the F_1 asci are 8-spored. Therefore, one could say 8-sporedness is dominant. But, as it

appears, 4-sporedness as contrasted with 8-sporedness must be regulated in this case by several pairs of factors working together. The resultant effect, then, may be only an apparent dominance. And so with dominance in haploid heterocaryons.

DICARYOTIC HAPLOIDS VERSUS DICARYOTIC DIPLOIDS

For many years past it has been a very common practice for botanists to refer to the ascogenous hyphae, and the dicaryophyte phase of rusts and mushrooms as diploid or sporophytic. There was good reason for calling the ascogenous hyphae diploid in those days when the theory of a double fertilization in Ascomycetes was so commonly accepted in America and England. For some of us it furnished an excuse for homologizing the outgrowths from the ascogonium with the ooblastema filaments of the red algae. Even after it was proved genetically that the nuclei of the ascogenous hyphae could not be diploid, we find authors still insisting that all such dicaryons in the fungi are *diploid*, even redefining the term to make it more nearly conform to their views.[3] We have discussed this practice at various times and more recently along with other items (**1942**; Dodge and Appel, **1944**). It was brought out again that to call cells diploid, tetraploid, or polyploid accordingly as they have two, four or many haploid nuclei, is incorrect. To say that a dicaryotic or heterocaryotic mycelium is a hybrid structure is misleading. We could perhaps say prohybrid, protohybrid or pseudohybrid, but not *hybrid*. Man can separate or isolate the two haploid components of a dicaryon. The isolated component races are nothing more nor less than the ones which originally paired to form the dicaryon. Man cannot separate or isolate two genomes once they have been brought together in a fusion nucleus. It would be to defeat the great principles of evolution if, at meiosis, the identical genomes or idential combinations of genes were to come out intact after reduction, especially where the diploid fusion nucleus is extremely heterozygous.

The mushroom fruit body. Jackson (**1944**, p. 11) again takes me to task: "Dodge's statement (**1939**) that 'The larger part of

[3] Professor Weiss (see footnote 2) has something to say on this point also. "Use of the same term in different meanings by different authors is a common source of controversey, leads to polemics and should be eliminated."

the fruiting bodies of mushrooms and Ascomycetes are haploid, therefore, we should not use the term hybrid to describe a mere mingling of hyphae or nuclei of two different races to form the framework of such structures . . .' indicates a fundamental misconception of the difference between the fruiting bodies of these two groups." "The mushroom," he says, "is totally the product of the dikaryotic diploid phase and with its supporting tissue is comparable to the dikaryotic diplont of the long-cycled rust." Now, we will all agree absolutely with this statement provided he will only substitute for the incorrect and misleading phrase "dikaryotic diploid," the correct and unimpeachable phrase "dikaryotic haploid." The dicaryophyte phases of the fungi are unique and highly important genetically. Why haul down our mycogenetic flag and try to warp the facts to make the dicaryon something that it is not? Our author realizes that everything is not crystal clear when he says, ". . . it is evident that the dikaryotic diplont of the rust and other Basidiomycetes may be compared with the F_1 generation of other organisms having a *true* diplont." [Italics mine.] Now that heterocaryosis in the fungi is proving of such great significance we can say "heterocaryotic haploid" and "dicaryotic haploid" and in this way avoid all argument. For years, Prof. F. J. Ryan of Columbia University informs me, protozoologists have been familiar with certain species of *Protoopalina, Zelleriella* and *Giardia* that are normally provided with two nuclei, each nucleus being diploid. *Paramoecium aurelia* has two diploid nuclei in addition to the macronucleus. Have biologists called such organisms *"tetraploids"* or *"dicaryotic tetraploids"?* No. They look upon them as *binucleate diploids*. They could, if they wished, call them dicaryotic diploids and be correct.

Kerl (**1937**), in a paper which Jackson evidently overlooked, reports that she dissected out, and studied the growth, or regeneration, of antheridia, ascogonia, trichogynes and ascogenous hyphae of *Pyronema*. She has the answer for a statement made earlier (Dodge, **1932**) as a probability, namely, that if one dissected out young antheridia, and if they were not too highly differentiated, they would produce mycelia with both antheridia and ascogonia. The same for ascogonia. Kerl was unable to obtain

regeneration of ascogenous hyphae, showing that the differentiation leading to ascus formation had gone too far so that reversion to a vegetative type of growth was no longer possible. Those who still hold to the theory of a double fertilization in *Pyronema* could say that Kerl's work proves that the nuclei of the ascogenous hyphae are actually diploid. Therefore, their cells could not regenerate. Dodge and Appel (**1944**), however, refer to a regeneration or vegetative growth of the ascus crosier of *Pezizella Lythri* observed many years ago.

Jackson's footnote No. 3 ends as follows. "In the interest of clarity students of the genetics of fungi might well adopt the system of symbols devised by C. E. Allen (**1924**, **1925**) for use in the Bryophytes." This is an excellent suggestion and it is one I made many years ago (**1928**, p. 5). I erred at that time in including the ascogenous hyphae in the F_1 generation and in referring to the f_1 mycelia as hybrid mycelia. In mating *N. tetrasperma* + *N. sitophila* the ascogenous hyphae that are first developed still contain the parental nuclei p_1 (A) and p_1 (a) intact and still separate, though in the same cytoplasm. The F_1 diploid generation is limited to the heterozygous ascus. The f_1 haploid generation would include the ascospores formed in the F_1 ascus, mycelia from these f_1 ascospores, conidia, spermatia, or microconidia, incipient parithecia with their ascongonia and trichogynous outgrowths and, finally, the dicaryotic ascogenous hyphae. Since in this interspecific cross the F_1 zygote is extremely heterozygous, the f_1 races are all quite unlike either parent, but they are not thereby hybrid. They are haploid segregates.

As we interpret Professor Jackson's views set forth in his address, we all agree with him that the fusion of two nuclei in the smuts, mushrooms, Mucoraceae and yeasts, would also constitute a sexual reproduction. He could very easily have completed his fine set of diagrams by including diagrams of life cycles, one each, of the Exoascaceae, yeasts, smut fungi, and mushrooms, where sex organs, as we understand them in the fungi, do not exist. We would also have appreciated a diagram of the life cycle of *Gelasinospora tetrasperma.* These added diagrams would have made perfectly clear his conception of sex in these groups. One

wonders why he omitted the +/− symbols in the diagrams of the life cycle of *Sclerotinia Gladioli* after having used these symbols to designate the two kinds of thalli in *Puccinia graminis*.

As a closing statement regarding my present views on mycogenetic terminology, I can not do better than to quote from an earlier paper (**1936**). "If one is able to work out a terminology that will more exactly express the situation in these fungi, instead of adding to the confusion with glittering generalities we shall be grateful. In the meantime, if we must be inconsistent, let us be inconsistent where it will serve a useful purpose."

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NOTES ON A PROPOSED NEW GENUS AND FOUR NEW SPECIES OF THE USTILAGINALES[1]

George L. Zundel

1. A proposed new genus

In 1893[1] Peck described a new species of smut collected by Dr. C. L. Shear on *Waldsteinia fragarioides* (Michx.) Trott. at Alcove, New York, to which he gave the name *Urocystis Waldsteiniae*. His original description is as follows: "Sori large, oblong, following the nerves of the leaf, commonly near the margin and nearly parallel to each other, surrounded by the ruptured epidermis, black; spores not easily separable, three to six or more in a glomerule, the central and peripheral similar, subglobose or elliptical, often angular, .005 to .006 inch long, .0004 to .0005 broad, the glomerules very unequal in size and in the number of component spores. On living leaves of barren strawberry, *Waldsteinia fragarioides.*"

In 1900[2] Ellis and Everhart described a new smut species collected by Robert M. Horner (No. *1430*) at Waitsburg, Walla Walla Co., Washington, on *Geum ciliatum* Pursh., to which they gave the name of *Urocystis Gei* Ellis & Ev. with the following description: "Sori epiphyllous, bullate, elongated, .5–1 cm., opening along the middle as in *U. Anemones,* forming by the inflated epidermis; central spores polar, subglobose, 12–16 μ diam.; peripheral spores darker, slightly granular-roughened, globose, 10 μ diameter, or ovate, 10 × 6–7 μ."

It must be noted at this point that Clinton[3] considered the above mentioned two new species as one and the same, using the name *Urocystis Waldsteiniae* Peck. In 1895 Otto Pazschke issued this

[1] Ann. Rep. State Botanist of the State of New York **1893**: 32. 1893. (From 46th Rep. of the N. Y. State Museum of New York.)

[2] Bull. Torrey Club **27**: 571–578. 1900.

[3] Proc. Boston Soc. Nat. Sci. **31**: 447, 448. 1904.

smut in Rab.-Wint.-Paz. Fungi Eur. *4011* under the name of *Ustilago Waldsteiniae* Paz.

Clinton in 1904 [3] and in 1906 [4] includes this smut in the genus *Urocystis* with the following note: "The generic position of this species is unsettled, but it is placed here until further study determines its place." Clinton [3] had previously reported in his Harvard thesis that Thom had determined that this species germinated as a *Ustilago*. Hansen and Atkinson [5] confirmed the findings of Thom in 1938.

Clinton [3] in 1904 wrote concerning this species as follows: "This fungus is peculiar in that while it has the general aspect of an *Urocystis* its position under this genus is somewhat doubtful since it lacks the peripheral layer of sterile cells. Neither does it seem to be a true *Ustilago*, as considered by Paszschke, since the spores adhere in pairs or small groups. The species needs further study, especially of the formation and germination of its spores, to determine its true generic position. The spores that adhere in pairs have the appearance of *Schizonella*. Often some of the largest spores appear to be sterile cells merely. The species described by Ellis and Everhart on *Geum* is not distinct."

From a study of the literature and of available specimens the writer has decided that this smut belongs to an undescribed genus of the family Ustilaginaceae Schröt., and proposes the following name in honor of his former teacher at Cornell University, Herbert Hice Whetzel, with the following description:

Whetzelia Zundel, gen. nov.

Sori in the leaves, following and infecting the veins, swollen, covered by an indusium of epidermal tissue which on maturity splits longitudinally dividing the sorus in two nearly equal parts and exposing a conglutinated spore-mass; spores produced singly or in indefinite spore-balls in pairs, triplets or sometimes quinate, rarely more; single sterile cells rare but sometimes attached to the spore-balls, lighter color than the fertile spores; germination as in *Ustilago*.

Soris in foliis venas inficientibus, tumefactis et indusio epidermidis tectis, soris indusio maturo rupto fere dimidiatis et massam sporarum conglutinatam

[4] N. Am. Flora **7**: 55. 1906.
[5] Phytopath. **28**: 8. 1938.

detegentibus; sporis singulis vel globis variis, binis, trinis, aliquando quinis, raro pluribus; cellis singulis sterilibus raris, aliquando massae sporarum adjunctis, colore clarioribus quam sporis fertilibus; germinantibus ut apud Ustilaginem.

One species, *Whetzelia Waldsteiniae* (Peck) Zundel.

Recently smut specimens received from Colombia, Guatemala and Hungary have been studied and appear to be new species as follows:

1. **Ustilago concelata** Zundel, sp. nov.

Sori destroying the inflorescence, 2½ to 3 mm. long, concealed by the leaf sheath, spore-mass dark reddish-brown surrounding the rachis as a powdery mass; spores globose to subglobose, regular, light reddish-brown, smooth, thin epispore.

Soris inflorescentiam perdentibus, 2.5–3 mm. longis et vagina folii celatis, massa pulverulenta sporarum fusce rubro-brunnea rachidem cingente; sporis globosis vel subglobosis, regularibus, dilute rubro-brunneis, levibus, episporo tenui.

On *Ischaemum latifolium* (Spreng.) Knuth. Coll. C. Garces O, "La Normal," Medellin, Colombia.

2. **Ustilago Garcesi** Zundel, sp. nov.

Sori as short striae on the leaves which finally cause a shredding of the foliage; spores globose to irregular or angled, reddish brown, 8.5 to 10.5 μ diameter, smooth and granular under immersion lens.

Soris in foliis breviter in strias dispositis, foliis ipsis denique minutatum scissis; sporis globosis vel irregularibus vel angulatis, rubro-brunneis, 8.5–10.5 μ diam., levibus et granularibus immersione ut dicunt olei visis.

On *Paspalum saccharoides* Nees, Palmira (Valle, Estacion Experimental), Colombia. Coll. C. Garces O, Dec. 13, 1940—Fungi of Colombia *1281*.

3. **Urocystis Ungeri** Zundel, sp. nov.

Sori as elongated striae in the leaves, somewhat pustular, grayish, covered by a membrane of host tissue; spore-balls globoid, chiefly irregular, consisting chiefly of one fertile spore, rarely two, completely surrounded by light reddish-brown sterile cells, chiefly 17.5 to 24 μ in diameter; spores globose to subglobose, dark reddish-brown, chiefly 12.7 to 18 μ diameter, smooth.

Soris elongatis striatisque in foliis, sub-pustularibus, canescentibus, membrana hospitis tectis; massa sporarum globoidea, plerumque irregulari, singulis praecipue fertilibus sporis, vel rariter binis, cellis sub-rubro-brunneis circumdatis, 17.5–24 μ plerumque diam.; sporis globosis vel subglobosis, fusce rubro-brunneis, 12.7–18 μ diam., levibus.

Hab. in *Polygonato multifloro* (L.) All., "Doubrava," Moravia, Coll. Bubak, 14 Mai. 1898; Budapest, Coll. Dr. G. von Moesz, 1 Jun. 1929.

Descriptio nostra facta est de duobus speciminibus, quae ex Moravia Hungariaque recepta titulos tulerunt *Tuburciniae paridis* (Unger) Vestergen. Investigata autem male determinata videntur, quapropter nova species hic proponitur atque describitur.

On *Polygonatum multiflorum* (L.) All., "Doubrava," Moravia, Coll. Bubak, 14.V.1898; Budapest, Coll. Dr. G. von Moesz, 1.VI. 1929.

The above description is based on two specimens received from Moravia and Hungary both labeled *Tuburcinia paridis* (Unger) Vestergren. Upon examination it was revealed that the determinations were apparently in error and therefore a new species is tentatively proposed and described.

4. **Entyloma Tagetesium** Zundel, sp. nov.

Sori in the foliage, distinct, pustulate and globoid, light colored, ½ to 1 cm. diameter; spores packed in host tissue, globoid or angular by compression, tinted reddish-brown to hyaline, 10.5 to 14 μ diameter, epispore 0.5 to .75 μ thick.

Soris in foliis, distinctis, pustulatis globosis, colore diluto, 0.5–1 cm. diam.; sporis dense in hospite compactis, globosis vel compressione angulatis, rubrobrunneis vel hyalinis, 10.5–14 μ diam., episporo 0.5–0.75 μ crasso.

On *Tagetes* sp., Chimaltenango, Guatemala. Coll. Albert S. Müller (No. *188*), Aug. 28, 1942.

ACKNOWLEDGMENT

The willing coöperation of Dr. Robert E. Dengler, Professor of Classical Languages, The Pennsylvania State College, who wrote the Latin descriptions, is hereby gratefully acknowledged. Any errors are to be charged to the oversight of the author.

CONTRIBUTION FROM THE DEPARTMENT OF BOTANY,
THE PENNSYLVANIA STATE COLLEGE NO.

NOTES ON BOLETES. VII

WALTER H. SNELL

(WITH 1 FIGURE)

Most of what follows was first put in manuscript form two or three years ago and has lain all but forgotten because of the distractions, new duties and changes in one's life brought about by the war. A brief respite during the summer months, however, has provided opportunity to prepare these notes for publication.

CORRECTIONS AND CHANGES

In Mycologia **33**: 422. 1941, the species *californicus* Murr. was placed in *Gyrodon* as a new combination. This change was an unfortunate error, for study of the type-material shows that Murrill had it correctly placed in the genus *Rostkovites* of his system or the more recently proposed *Suillus* (= *Ixocomus* Quélet = the Viscipelles of *Boletus* of Fries and Peck—see Mycologia **34**: 406. 1942). Not only do the spores place this species in the old Viscipelles of *Boletus* (or the genus *Suillus*) but also the glandular-dotted tube-walls and mouths, and stipe. The surface of the pileus is very fibrillose-tomentose to more or less fibrillose-scaly and is probably more or less viscid under moist conditions.

All these characters immediately remind one, however, of the species *hirtellus* Peck (= *tomentosus* Kauff.) and especially its more fibrillose-patchy to fibrillose-scaly variety *mutans* Peck. The only differences are the much more tomentose or fibrillose condition of the surface of Murrill's species and the spores slightly larger (8–11.5 × 3–4.5 μ as against 7–11 × 2.5–3.5 μ) and slightly deeper olivaceous. While heretofore no collection of *hirtellus* or its variety *mutans* has been seen with these extremes of surface clothing and of spore size and color, nevertheless it appears that *californicus* belongs in the *hirtellus* complex. Therefore, until more collections than the type are available for determining

whether Murrill's collection is only an extreme variation of *hirtellus* or definitely distinct, *californicus* will be considered as a form of *hirtellus*.

In Mycologia **33**: 26. 1941, a roseate *Boletinus* from Washington was named *forma rubrotinctus* of *B. cavipes*. Further study seems to show that this is *B. ochraceoroseus* Snell.

FOUR SPECIES OF SUILLUS

In the genus *Suillus* there are some groups of species which have probably proved perplexing to every collector of the Boleti. Two of these groups have the species centering around two of the longest recognized species—*S. luteus* (L. ex Fr.) S. F. Gray and *S. granulatus* (L. ex Fr.) Kuntze (or what has commonly been accepted as this species in America from the very beginning of mycological collecting). Peck thought he understood the species in question, but subsequent workers have had their doubts about specific validity. While I myself agree with Peck with confidence, on the other hand every so often in wakeful hours in the dead of night I have wondered if some species so sharply distinguished in written descriptions might not really be variational responses to differing conditions of climate, soil, water and rain, mycorrhizal host, and so on. Accordingly, it was very reassuring recently to find almost perfect conditions for confirming one's convictions with regard to some of these species.

The fall of 1942 was not particularly rainy in southeastern New England, but in the first half of October certain localities were replete with fleshy fungi. For example, at Centerville on sandy Cape Cod (part of the Commonwealth of Massachusetts, for the benefit of those unacquainted with New England's "stern and rock-bound coast"), many practically pure stands of pitch pine contained thousands of fruit-bodies. On October 4th, 95 per cent of these were *Leccinum versipelle* (Fr. *apud* Hök) Snell [or *L. aurantiacum* (Bull. ex Rocques) S. F. Gray, as it may turn out to be]. On October 18th, fully half of these were this same species, but at least four Suilli made up most of the remaining half, with a sprinkling of agarics, clavarias and puffballs. These four species grew clumped in colonies over large areas in places,

and elsewhere pretty well mixed. In one spot, one specimen of each of three species grew in a triangle about 15–18 inches on a side.

The species were two pairs—*S. luteus* and *S. subluteus* (Peck) Snell, and *S. granulatus* and *S. brevipes* (Peck) Kuntze. As

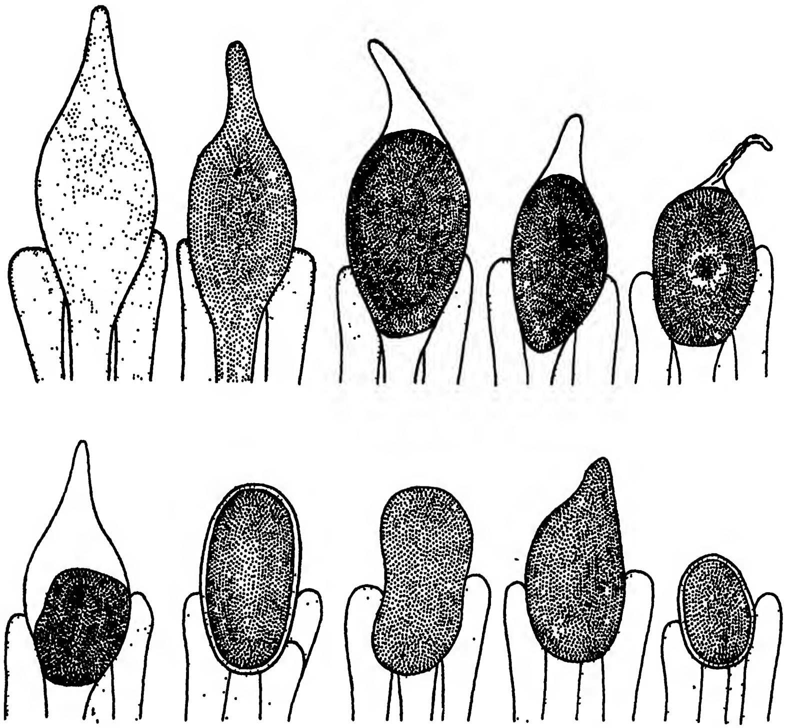

FIG. 1. Arrangement of drawings in putative sequence showing the formation of brown bodies in the hymenium of certain *Boleti* by the possible degeneration of cystidia, × 1000.

seen from above, the pilei of all four species looked about the same even to a practiced eye. About the only differences that were superficially obvious were that *S. luteus* was a little thicker and more rounded-pulvinate and that the gluten of *S. brevipes* was more copious and tougher, often giving a grayish or lurid or sallow color.

Closer examination of the first species confirmed the differences which have appeared to be sufficiently constant. I have always

found the pileus of *S. luteus* rounded-pulvinate to something approaching umbonate and therefore with flesh comparatively thick, while *S. subluteus* is at best plano-convex and usually more or less applanate, with margin often repand, and with correspondingly thinner flesh as described. The tubes of the former species were darker and more orange and smaller and more reddish-glandular-dotted, those of the latter more pale yellow, a little larger and much less glandular-dotted. Also as described, the veils and annuli differed. The veil of *S. luteus*, even when retracted so that it did not entirely sheath the stem, was much more extensive on the stem and formed a prominently flaring annulus, while the veil of *subluteus*, even though in some of these specimens more extensive on the stem than I have observed before, was collapsed to form a decidedly glutinous band which was flaring only occasionally and to a slight extent. The color differences also were distinctive except in an occasional specimen. More especially, many of the stipes of *luteus* were very orange-buff, the flesh of the pileus and stipe was the same and at the base of the stipe more orange to light or deep Indian-red.

Similarly, *S. granulatus* and *S. brevipes* could be easily distinguished on the basis of the commonly described characters, even though in this case the color of the pileus of *brevipes* was about the same as that of *granulatus* except for the usual difference imparted by the thick tough gluten. The stipe of *brevipes* was of course short and stocky, was inclined to have less yellow and especially less inclined to have the yellowish apex of *granulatus*, had fewer and more inconspicuous glandular dots, and also was decidedly reticulate in a narrow zone at the very apex from the descending walls of the tubes, or undulately wrinkled in a conspicuous manner as contrasted with *granulatus*. The spores of *S. brevipes*, as described, in these specimens, were mostly over 8 μ long instead of mostly 7 μ or under for *granulatus*.

Hence, the conclusions arrived at from different studies of scattered collections at different times were beautifully substantiated by the unusual co-existence of these four species in a single habitat. It was particularly gratifying to find *granulatus* and *brevipes* in the same place at the same time. I have found *granulatus* occasionally very late in the fall but I have never found

brevipes at other times than from the very last of September until November 1st, as Peck originally stated in general as "very late in the season." I had often wondered if *brevipes* might not be only a form of *granulatus* stimulated by lower fall temperatures, perhaps by frost.

As a footnote to the foregoing, one other observation might be added. Peck described *Boletus albidipes* [which would now be **S. albidipes** (Peck) Snell, comb. nov.] as having a paler pileus, with conspicuously appendiculate margin, white flesh, stipe white without yellow and not dotted, and larger spores. I once found a young stage which appeared as if it might be this species, especially because of its copious, cottony, marginal tissue, but on the other hand I have also seen mature *granulatus* with something of this character. At Centerville on October 18th, 1942, I found several specimens among the other four species discussed above which had the *albidipes* characters in varying degree. It perhaps is not proper as yet to decide to give up the hope that a good *albidipes* will be found at some time, but on the other hand the recent specimens indicate that such forms are only extreme variations of the old species.

SOME OF THE LURIDI

It is going to take quite a bit of working over to solve all the problems of this group and therefore only a few remarks are made here.

Boletus magnisporus Frost apparently is a very rare species. It should be readily recognizable, with its golden-yellow pileus and red and yellow stipe, but few have reported it. I have never collected it. The spores of Frost's specimens at Burlington, Vermont, were as described—10–22 × 4.5–9 μ, mostly 14–16 × 5–5.5 μ—but I found the spores of the supposed type or co-type at the Farlow Herbarium to be 9–12 × 3–3.5 μ—hardly "large-spored."

Boletus firmus Frost is another species which has not been studied carefully because of its rarity. Krieger was certain he had it from Canada (The Mushroom Handbook, 1936, p. 265). I have found the following variations in spore measurements: the

type in the Frost Herbarium at Burlington, Vermont—9–12 × 4–5 μ; supposed type or co-type at the Farlow Herbarium—9–12 × 2.5–4 μ; specimens so labelled at Albany, N. Y.—11–15 × 4–5.5 μ.

There has been a great deal of misunderstanding in this country concerning the common member of the Luridi with the conspicuously furfuraceous stipe. Many collectors and workers have failed to distinguish between the species with reticulate stipe and the one with the furfuraceous stipe, and have called everything of either sort *B. luridus* Schaeff. ex Fr. Others have called specimens with furfuraceous stipe var. *erythropus* of *B. luridus.* A few have considered the mealy-stiped entity a distinct species, the same as the European *B. erythropus* Fr.

Very few have reported finding Peck's *B. subvelutipes,* a species characterized as having the stipe "*velvety with a hairy tomentum toward the base*" (Peck, Boleti of the United States, 1889, p. 142) —partly perhaps because they expected to find specimens with a lot of conspicuous tomentum on the stipe. I myself was misled at first by this erroneous conception, and especially later after I saw in Peck's folders at Albany a water-color drawing of specimens with stipe having a yellow apex, the remainder pale reddish-purplish with red mealiness, and a copious and conspicuous mass of brown velvetiness or tomentum extending about an inch up from the dirt at the base. I got in the habit of looking for specimens with these striking characters and never found them. Many perhaps followed Murrill (North American Flora **9**: 151. 1910) in considering *subvelutipes* as the same as *luridus* (including *erythropus,* or what had passed for it, if it was considered at all).

When one began to look at his collections of the common species with red tube-mouths and furfuraceous stipe at all carefully, however, it was found that they all had a greater or lesser amount of a coarse velvetiness or tomentum or strigosity at the base of the stipe, perhaps more or less underground or in the debris at the base, not brown in color but a rich buff-yellow or deep red. Sometimes there was only a very small patch of this velvetiness and rarely it was reasonably extensive and conspicuous, but it was always there. One began to suspect that he was dealing all the time with *subvelutipes* and not with the European *erythropus*

at all. A study of Peck's specimens at Albany, some labelled *subvelutipes* and some *erythropus,* disclosed the same velvtiness at the base of the stipe in all of them, only a small patch in some cases and in one specimen, as I recall, with this clothing extending for a distance of two inches.

Accordingly, nearly ten years ago, I came to the conclusion that our common member of the Luridi with furfuraceous stipe was Peck's *subvelutipes* and not the European *erythropus* in any sense, and I have been accustomed so to identify specimens sent by numerous collectors over the country.

The question naturally arises then—do we have in this country anything comparable to the European *erythropus?* I can add only the following remarks. Under some hemlocks near Bridgewater, Vermont, in 1932, I collected some fairly large specimens badly infested with eelworms (see Mycologia **26**: 358–359. 1934), which I determined with some puzzlement as *B. erythropus* but which were entirely different from what had been commonly known by this name (now *subvelutipes*). They were much more yellow on the pileus and stipe, with only a little red on either and no rich brown on top, and the tube-mouths were only partially reddened. As I have thought of them since and compared them with European descriptions and colored illustrations, they look a great deal like *erythropus,* but I would hesitate to declare that they are. Further, I have had some correspondence and exchange of water-color drawings with Paul Marshall Rea of Santa Barbara, California, as a result of an original, tentative identification of certain specimens as Peck's *subvelutipes.* Some of Rea's specimens are small and relatively slender like the smaller sort of specimens of *subvelutipes* in the east, while others are very stocky and thick, with very ventricose stipe. All I can say at the present moment is that I do not know what species of this group they have in California, but that it is possible that *erythropus* occurs out there.

NOTES FROM FROST'S HERBARIUM

Frost, the "Shoemaker Botanist of Brattleboro, Vermont," must have worked under rather difficult conditions—without much literature, without herbaria for purposes of comparison, apparently

without much except some sort of contact with Charles H. Peck. Nevertheless, he effected some very solid accomplishments with the Boleti. He apparently had a very good eye for new species and he originally described many more than are now recorded to his credit for the reason that he found that Peck had anticipated him in a goodly number. Frost left behind him, exclusive of specimens now in the Farlow Herbarium or in Peck's Herbarium at Albany, a fair-sized herbarium of fungi, which is now preserved at the University of Vermont. This herbarium is in much better condition than was expected from reports—much better than could be expected when one learns that for many years before it was obtained by the University of Vermont, it was stored in an attic, unprotected against extreme changes of temperature, insects, mice, occasional leaks in the roof and so on.

On a visit to the Frost collections in the summer of 1941, the present writer was delighted to find so much in such good condition. Doubted and abandoned species were there as well as the types of common and well-understood ones. All were examined more or less completely, but some unfortunately not completely enough to answer the innumerable questions which have come to mind in the succeeding months. Some of the fruits of this pilgrimage are given below.

It was suggested (Mycologia **33**: 26. 1941) that Frost's description of *B. ferrugineus* would fit *B. pseudodecorus* Snell and Dick. Comparison of specimens of the latter with Frost's types confirm the suspicion that they are the same. Contrary to what was said erroneously in the above-mentioned article, Frost's name is valid under the International Rules and *pseudodecorus* drops into synonymy.

B. sordidus has not been at all understood since it was named by Frost from Vermont. Peck records it as collected elsewhere only by Morgan in Ohio. As far as the writer knows, no one else has collected it with certainty. Its description reads much like two species at least for the present placed in the genus *Porphyrellus*—*P. porphyrosporus* (Fr.) Gilbert and **P. fumosipes** (Peck) Snell, comb. nov. The main differences in the descriptions are that the spores of *sordidus* are given as yellowish-brown to dirty brown in deposit, while the other two species have spores purplish-drab or

porphyry-reddish to purplish-brown in deposit, and that *fumosipes* has a rimose-areolate surface while that of *sordidus* is even. I along with others have often wondered if *fumosipes* and *sordidus* are not the same, and Coker and Beers (The Boletaceae of North Carolina, 1943, pp. 71, 72) have decided that they are and call the single species *sordidus*. This may be the proper disposition of the difficulties but I still want to convince myself by finding the answers to a few questions. The difference in the surface of the pileus has run true to form in my somewhat limited experience with the complex, as has also a difference in spores.

A few years ago, the writer found a single specimen labelled *sordidus* in Peck's herbarium at Albany, but since then it has been rather elusive and the writer had begun to lose confidence in the specimen and in his observations of its spores. Study of Frost's types at Burlington in 1941, however, resulted in some very clear convictions. The original description reads a little more like that of *fumosipes* but the dried specimens look more like *porphyrosporus* than *fumosipes*. The spores, however, appear to be quite distinctive. They are shorter than those of *porphyrosporus*, the majority are even a little shorter than the majority of *fumosipes*, and they are as broad as those of *porphyrosporus*. They are less inclined to be subfusiform than those of the other two species, and more amygdaliform than elliptical or subelliptical, and they are a deep, dull brownish-yellow in color, with homogeneous contents, instead of with reddish outer contents and a greenish center as in the other two species as I have understood them. The spores are therefore quite distinctive—in form from any other species of Boleti and in deposit from the two species which they seem outwardly more or less to resemble.

Even though the genus *Porphyrellus* remains to be more precisely defined, the facies of the species *sordidus* and its spores definitely suggest a close relationship with the other two species of the genus and accordingly, it will be so placed at least for the present, as **P. sordidus** (Frost) Snell, comb. nov.

Boletus limatulus was for a long time as much of a puzzle as several other species of Frost's, until some of its odd characters brought to mind some unusual specimens collected by the writer at McCollums, N. Y., a few years ago. These specimens were

first seen under a white pine when very small and because of their peculiarities and dissimilarities from the well-known species under white pine they were followed in their development until maturity, even at the inconvenience of several long trips by car just for this purpose. These were finally determined, with a slight tinge of irritation at the time, energy and gasoline spent, as merely a variant form of *Xerocomus badius*. They were characterized by yellow-brown color instead of bay, by the tube-mouths here and there thickened and colored yellowish-brown to reddish-brown, by cystidioid structures, and by spores often a little larger, especially a little broader. In his characterization of *B. limatulus*, Peck described the pileus as "*viscid when moist*, somewhat polished and shining when dry, rich yellowish brown, flesh *reddish in the pileus* . . . ; tubes . . . greenish yellow, their mouths yellowish brown . . . ," and below remarked that although the differently colored tube-mouths made the species approach the Luridi, it would be placed in the Edules because the mouths were not red or reddish. It appears that Frost's species should be considered as a variety of the Friesian—*Xerocomus badius* (Fr.) Gilbert **var. limatulus** (Frost) Snell, comb. nov.

Boletus tenuiculus is a very slender-stemmed species described as having both pileus and stipe "lurid-red on a yellow ground." While there is no unanimity as to the precise meaning of "lurid," it appears that the older workers used the word in the sense of pale or sallow or dingy or sordid. Of a few more or less well-known species of which *tenuiculus* might be a long-stemmed form, the color description perhaps best applies to Peck's *B. fulvus*. This species sometimes has a stipe which is quite long and rather slender, although the pileus is not "thin" as given in the original description of *tenuiculus*, but neither are the pilei of some of Frost's specimens. On the basis of information available at present, however, it does not appear desirable to suggest any changes.

Boletus innixus also has many of the characters of *fulvus* or *tenuiculus*, and the dried specimens look a lot alike, although the spores of *innixus* are a little small and the surface is more fibrillose to possibly bunchy-fibrillose. This latter character suggests Frost's *Roxanae* [**Xerocomus Roxanae** (Frost) Snell, comb. nov.], although Frost thought they were different species, since

he published the two new descriptions in the same article, practically side by side.

Boletus unicolor was so named by Frost (in Peck) because it is yellow within and without. So also are *Suillus americanus* (Peck) Snell and *S. subaureus* (Peck) Snell. Peck distinguished *unicolor* from these two latter species by the absence of glandular dots on the stipe. He suggested a varietal relationship to *bovinus* but felt that the colors of the tubes and spores required a separation of the two. The dried specimens of *unicolor*, however, do show the presence of glandular dots on the stipe nearly to the base and to a certain extent on the tubes. This character would remove *unicolor* from any close relationship to *bovinus*, but from the description and the dried specimens, it is difficult to determine whether or not *unicolor* could be either of the Peckian species. The spores are nearest to those of *americanus* but the stipe is thicker than it ordinarily is for that species, except in rather large specimens. In deposit, the spores are given as reddish-yellow—obviously inaccurately, for a spore-print of this color would be very strange in the genus *Suillus* or any other genus of the Boleti but one, and even for Singer's new genus *Xanthoconium* (Peck's *B. affinis*, etc.) with spores in mass ferruginous-ochraceous, the term is nowhere near precise.

In view of the inadequacy and inaccuracies of description of *unicolor* and the difficulties mentioned, it at present appears neither possible to assign the epithet to synonymy nor desirable to maintain a third all-yellow species of *Suillus*. A satisfactory disposition of the name other than that of dubiety for the present will have to await the uncovering of further information.

On the other hand, another of Frost's species, *B. decorus*, cannot be correlated in any way with any other known species and even though it has not with certainty been identified by anyone since Frost, it must be considered as good until something resembling it can be collected or until other information is available.

BOLETINELLUS POROSUS

Murrill long ago changed the name of the familiar and easily identifiable *Boletinus porosus* (Berk.) Peck to *Boletinellus meruli-*

oides—a new genus for this somewhat odd species and the specific name of a *Daedalea* given by Schweinitz. The writer has been slow, perhaps unduly so, in accepting Murrill's combination until recent studies were completed. As noted previously (Mycologia **33**: 421. 1941), Singer would place this species in *Gyrodon* and reduce *Boletinellus* to synonymy, but the writer prefers at least for the present to retain it. In any event, Schweinitz's specific name must be accepted in place of Berkeley's, which was likewise used by Peck. A few years ago, the Schweinitz Herbarium at Philadelphia was searched for odd items, and along with other interesting ones, a very small piece of what must be the type specimen of Schweinitz's *Daedalea merulioides* was found. There is very little left but a piece of the tube layer, but there is enough to provide an abundance of the spores that are entirely peculiar to this species. Therefore, *Boletinellus merulioides* (Schw.) Murrill replaces *Boletinus porosus* (Berk.) Peck.

BOLETUS POCONO SCHW.

Schweinitz described this species from specimens collected in beechwoods in the Pocono Mountains of Pennsylvania (Synopsis Fungorum in America Boreali Media Degentium. Trans. Am. Phil. Soc. II. **4**: 314. 1832). The types are not available in Schweinitz's collection in the Academy of Natural Sciences in Philadelphia nor in the Michener collection in the Division of Mycology and Disease Survey at Washington. The original description is short and inadequate and apparently no one has ever been willing to make a guess as to what Schweinitz's species might be.

In the Michener collection, however, there is a specimen labelled by Michener as "*B. Pocono* ? N. Garden. C. Co. 1052 and 1063." "C. Co." means "Chester County." These specimens are in excellent condition and unquestionably are *Boletinus castanellus* Peck. There is no way of knowing whether Michener had any acquaintance with Schweinitz's *B. Pocono* which suggested this questionable identification of his fungus or if he merely made a tentative identification by means of the original brief description. At any rate, with Michener's lead it is easy to see that *B. Pocono*

might be what has long been known as *castanellus*. Even though there is no acceptable basis for a declaration of synonymy in this case, there is a certain amount of satisfaction in having some idea as to what Schweinitz's species might have been.

BOLETINUS PICTUS

Unfortunately it has fallen to my lot in my studies of the American Boleti to be compelled under the International Rules to make nomenclatural changes. Several changes have been particularly regrettable, since they have involved the abandonment of names known and applied for a long period of time by everyone in this country who has made collections of the group. The sort of change that I very much dislike to make, however, is to replace a very appropriate specific epithet with one that could be considered as nothing but a very poor one, the only virtue of which is its priority. And particularly the most painful duty is to replace an epithet not only of long standing but excellent in that it is accurately descriptive or has a pleasing flavor, even something of poetry in certain instances, with one that was manufactured as the genitive of the name of an individual. To me this practice is an abominable habit and has nothing to recommend it. I am happy that in one particular case the original discomfiture fortunately proved to have no foundation.

Everyone who has ever known any of the Boleti has been familiar with the common and beautiful *Boletinus pictus* Peck under our eastern (or northern) white pine. No one has questioned the validity of Peck's name, although privately the writer came to do so because of what seemed to be the plain and incontrovertible facts. Peck considered *B. Spraguei* B. & C. (Bull. N. Y. State Mus., vol. 2, no. 8, September, 1889, p. 77), and others have considered *B. Murraii* B. & C., to be the same. These two species of Berkeley and Curtis were published in Grevillea, vol. I, 1872, the September issue, pages 35 and 36, respectively. The description of *B. pictus* appeared on page 128 of the "Twenty-third Annual Report of the Regents of the University of the State of New York, on the Condition of the State Cabinet of Natural History," etc., which is usually abbreviated to read "Ann. Rep. N. Y. State Cab.," and the

commonly accepted date of publication has been 1872. On the other hand, as I looked up this publication in my own set of Peck's Reports, I found that the "Report of the Botanist" is signed on page 135 "Chas. H. Peck, Albany, *January* 8, 1870" and on the title page of the volume it is stated that the Report of the Regents was transmitted to the Legislature on March 10, 1870, but at the bottom of the title page, the printer's date is given as 1873. Accordingly, the situation seemed to be that the epithet *pictus* had been published in 1873 even though Peck had submitted the Report containing it in 1870, that the epithets *Spraguei* and *Murraii* had been published in September, 1872, and that even though Peck later had considered *Spraguei* a synonym of *pictus*, there was no alternative but to abandon the name *pictus* in favor of either *Spraguei* or *Murraii*—both repugnant, if not abhorrent.

Donald P. Rogers one day, however, called to my attention the presence of a discussion by Farlow on a shelf in the Farlow Herbarium of the varied manner in which Peck's Reports appeared, under various guises and with different datings. It was found that the copy of Peck's Report 23 for 1869 at Cambridge containing the description of *pictus* bears the date 1872. Then Homer D. House reported that after failing to get any satisfactory results from examination of official files, he looked at Peck's own set of Reports. Here he found that on Appendix C, "Report of the Botanist," it was stated "Printed in Advance of the Report" and that this advance printing of Appendix C is dated 1872. Further, the title page of Peck's copy of his Report has a date stamp on it which states that the printed copy was received in his office on March 23, 1872.

Therefore, it is obvious that the copy of Report 23 in my possession is the complete Report 23 of the Regents and that the advance printing of Appendix C, Peck's Report, establishes the priority of the publication of the description of *Boletinus pictus* over the epithets published in the September issue of Grevillea.

YELLOW-BROWN HYMENIAL BODIES

Yellow-brown bodies have been found in greater or lesser abundance in the hymenium of fruit bodies of the following species of

Boleti—*Suillus hirtellus* (Peck) Kuntze, *Xerocomus badius* and its variety *limatulus, Boletus griseus* Frost, *B. decorus* Frost (type specimen), *Tylopilus alboater* (Schw.) Murr., *T. indecisus* (Peck) Murr., and *T. plumbeoviolaceus* Snell & Dick. These have varied in size from what one would call ordinary-sized hymenial bodies, as compared with cystidia, etc., to quite large ones. They have varied in shape from spherical to oblong-elliptical to broadly fusoid or fusoid-ovoid to all sorts of modifications of these shapes to very irregular, if not almost amorphous in some cases. The first such bodies noticed were very irregular in shape and it was supposed that they were resinous residues of some sort, possibly resulting from the drying of fluids from lactifers or similar structures. They were found, however, to be insoluble in ordinary solvents. Then it was found that in certain species at least these bodies were mostly regular in shape—spherical or oval for the most part—and the more regular ones appeared to have a thick wall. These are still very puzzling and one cannot say with any assurance what their origin and nature may be, but in some mounts of tube-tissues can be found what appear to be stages in their formation and development. Figure 1 shows an arbitrary arrangement of structures found in a single mount. From left to right are represented a mature, ventricose-rostrate, hyaline cystidium ("lageniform" to the Europeans), one becoming yellow, the closing-off of the deep yellow-brown ventral body, the loss of turgidity of the hyaline neck, and finally some of the more regular dark yellow-brown bodies without any remains of the cystidial wall.

BROWN UNIVERSITY,
PROVIDENCE, R. I

NOTES AND BRIEF ARTICLES

A Correction

In the article "New and heretofore unreported species of the higher Ascomycetes from Colombia and Venezuela," published in Mycologia **36**: 429–459. 1944, on page 437, line 9, a serious omission occurs between "bifurcated (branches 9–12)." . . . and . . . "A new collection was made by the author . . . etc." The corrected version should read:

. . . bifurcated (branches 9–12 μ long). The perithecia are 125 μ in diameter, collapsing. The ascospores are 4-septate, elliptical with blunt ends and slightly constricted at the septa, measuring 32–34 × 12–13 μ.

This species differs from *M. Psychotriae* Earle in having some of the setae bifurcated and from *M. anceps* Syd. and from *M. anceps* var. *Mussaendae* (Syd.) Stev. in the character of the setae, many of which, in this material, are dark in their total length without having a pellucid tip. Other minor differences in the aspect of the mycelium and the hyphopodia are apparent when the specimen is compared with *M. Psychotriae* Earle (FV *306* and *372*) and with *M. anceps* var. *Mussaendae* (CUPP *32821* and *32907* from the Philippine Islands). The specimen is rather poor, many colonies being overrun by *Trichopeltaceous* and *Meliolicolous* parasites.

Meliola Obtusa (Toro) comb. nov.

Irenina obtusa Toro. Journ. Dept. Agric. Porto Rico **14**: 236. 1930. On *Tontanea canascens* (Willd) Stand.

Colombia, Antioquia, Road Medillin-Las Palmas, 2000 m., Garcés et al., Mar. 31, 1942. FC *1661*, Med. *408*.

A study of the type specimen (Toro FC *221*) discloses the presence of mycelial and perithecial setae, and consequently the species must be transferred to the genus *Meliola*. A new collection made by the author . . . etc.

The above error was due to the omission of one whole page in the manuscript sent to the press. The author's copy of the manuscript also lacked this page and the mistake unfortunately occurred at a point in the paper difficult to detect from the sense of the words alone; it was thus overlooked when the galley proof was checked.

CARLOS GARCÉS O.

UNIVERSIDAD NACIONAL FACULTAD DE AGRONOMIA,
MEDELLIN, COLOMBIA

MRS. G. MILLER

The retirement of Mrs. Miller from The New York Botanical Garden, for a domestic career, after nearly twenty years of service, is a great loss to MYCOLOGIA and to the Mycological Society of America. Even before the organization of the Society she was virtually an assistant editor. Among other things she, under the supervision of the writer, compiled the twenty-four year index to MYCOLOGIA, which has been found so useful to mycologists.

She is familiar with every step in the organization of the Mycological Society and its affiliation with The New York Botanical Garden, and personally acquainted with the many mycologists who have called at The New York Botanical Garden, during the past years. Since the organization of the Society, she has continued to act as assistant in both editorial and managerial matters. Her great care and insight into the financial details has "stopped many a leak," and saved much money both for the Mycological Society, and for The New York Botanical Garden.

On behalf of the Mycological Society of America our best wishes are extended to her for the future.—FRED J. SEAVER.

PATHOLOGY IN FOREST PRACTICE

This volume by Dow V. Baxter, Associate Professor of Silvics and Forest Pathology in the School of Forestry and Conservation in the University of Michigan, has recently appeared.

While the book is intended for use by the practical forester, it will be of interest to mycologists as well since considerable space is devoted to fungi destructive to forest trees.

The volume published by John Wiley & Sons is put up in the usual substantial form. It comprises i–xi + 618 pages and 232 figures. The illustrations are unusually good. A more detailed account of this work by Perley Spaulding may be found in the Journal of The New York Botanical Garden for December 1944. —FRED J. SEAVER.

Professor Whetzel in 1937 at the age of sixty

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HERBERT HICE WHETZEL

H. M. FITZPATRICK

(WITH 3 PHOTOGRAPHS)

In the death of Herbert Hice Whetzel, November 30, at Ithaca, New York, the mycologists and plant pathologists of America have seen the passing of one of their most outstanding figures. He was a distinguished scientist and a vivid, colorful personality. He died at his home on Forest Home Drive, at the head of Beebe Lake, where he had lived for more than thirty-five years beside the campus of Cornell University. For about six weeks he had been too ill to go to his laboratory, and though months earlier at a similar crisis he had made a remarkable recovery, his family and close friends realized that this time the end was near. The insidious malady that had sapped his strength was no longer to be denied. He had fought it courageously, with only occasional mention of the discomfort and pain that he suffered, and his fortitude will remain an inspiration to others who seek attainment against heavy odds. His colleagues in the Department of Plant Pathology will long remember his last years in which, with characteristic stoicism, he tried to ignore his physical condition as he increased his efforts to complete his investigations of the Sclerotiniaceae. He passed away at the age of sixty-seven, in the forty-second year of his days at Cornell. He lies buried at Ithaca in Lake View Cemetery, high on a hillside overlooking Cayuga Lake. The returning former student who seeks out the grave to stand in retrospection, thinking of his old professor, will be rewarded by an

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especially attractive panorama embracing the lake, the valley, and the circling hills. Professor Whetzel is gone. The beautiful countryside about Ithaca will not again see him searching for fungi in sphagnum bog or wooded glen. Yet in nearly every country and clime he lives in the memories of former students who received inspiration from him, respected him deeply, and loved him well.

It is especially fitting that a memorial article concerning Professor Whetzel be printed in *Mycologia.* He served on the editorial board of the journal for seven years, and contributed a considerable number of significant research papers to its pages. At the founding of the Mycological Society of America, in 1931, he was prominent in urging that *Mycologia* be adopted as its official organ of publication. He, more than any other, had favored the formation of the Society and should receive the major credit for taking the initial moves that led to its establishment. He remained actively interested in its affairs and, in 1939, was its president. He attended five of the nine annual summer forays held before the outbreak of the war, and no member collected more industriously and effectively, or contributed more to the success of those occasions than he. At the winter meetings he participated regularly in the sessions of the Society and frequently enlivened its business meeting with a characteristically vigorous presentation of some point about which he felt strongly. As he was long one of America's leading plant pathologists, it is appropriate that a memorial article be published also in *Phytopathology.* This has been prepared jointly by Dr. M. F. Barrus, one of his first students, and Dr. E. C. Stakman, his friend for more than thirty years. Appended to their paper is an approximately complete list of his publications. These number more than two hundred and, as most of them are not mycological in character, duplicate publication of the entire list here in *Mycologia* has seemed undesirable. A personal tribute to Professor Whetzel has been published by Dr. Barrus in the undergraduate journal, the *Cornell Countryman.* An official memorial statement has been prepared by Dr. L. M. Massey, and read by him before the faculty of the New York State College of Agriculture. It emphasizes Professor Whetzel's characteristics and accomplishments, and will be

incorporated by the University in its memorial booklet, "Necrology of the Faculty," which is printed annually for its archives and limited distribution.

Professor Whetzel was born, September 5, 1877, near the village of Avilla, in Noble County, in the northeast corner of Indiana. He was the son of Joseph Conrad Whetzel, born October 31, 1849, in Beaver County, Pennsylvania, and Gertrude (Eckles) Whetzel, born August 4, 1858, in Wood County, Ohio. They were married, October 26, 1876, at Avilla, and had six children, three sons and three daughters. When but a young boy, Joseph Conrad had come to Avilla from Pennsylvania with his parents, Joseph Whetzel and Susanna (Eichling) Whetzel, and had helped his father and brothers clear off timber and establish their farm. At about the same time Gertrude Eckles was brought by her parents from their earlier home in Ohio, where they had married, October 4, 1857. Her father, Valentine Eckles, was born, March 9, 1833, in Holmes County, Ohio, and died, August 12, 1892, in Noble County, Indiana. Her mother, Sarah Ann (Bronson) Eckles, was born in 1837, in Onondaga County, New York, and died, May 13, 1891. They were mainly of Scotch-Irish descent.

The Whetzels came from a line of Pennsylvania "Dutch" farmers. The family had originated in southern Germany, near the Swiss border, and reached America in about 1737. After settling in Maryland, they migrated north into eastern Pennsylvania, and from there some of them took part in the westward movement that occurred about the time of the Revolutionary War. One member of the family, a woodsman and trader, who lived before 1800 in the forest on the frontier near Wheeling, West Virginia, was killed by the Indians. His young sons, saw him scalped and their cabin burned. Though accounts differ as to the number and names of his children, one of the sons was the Lewis Whetzel who later became famous as a scout and frontiersman. He swore eternal vengeance on the redmen, and his name is connected with many thrilling episodes of the border warfare. Professor Whetzel claimed descent from a brother of Lewis, and on various occasions alluded with evident satisfaction to this branch of his family tree. The name Whetzel (written earlier Wetzel) had prominence in pioneer days in Indiana also. In 1818, Jacob Whetzel, brother

of Lewis, was living in Franklin County in the southeast corner of the state, a short distance northwest of Cincinnati. Having been granted a tract of land deep in the forest southwest of present-day Indianapolis he set out with his son Cyrus to blaze a trail to their new home. This trail, known in accounts of early Indiana as the Whetzel Trace, began at Somerset (now Laurel) on the White Water River, a tributary of the Ohio, and ran west through the wilderness to the White River, a branch of the Wabash. It ended at the spot now occupied by the village of Waverly. Returning for their families the Whetzels widened the trail, and the next summer drove in with their possessions. Their cabin, erected on the high bluffs overlooking the river, was the first permanent white habitation in Morgan County. Following them, the majority of the early settlers of central Indiana came in over the Whetzel Trace. As Professor Whetzel was pioneering in plant pathology, it pleased him to emphasize that there was much pioneer blood in his veins.

Up to the age of nineteen, his life was spent chiefly on his father's farm in Swan Township, five miles from Avilla. Records filed by him show that he attended the Hopewell country school, and graduated, in June 1895, from Avilla High School. He and a neighbor boy usually walked the five miles to and from school. We may picture him an energetic lad helping with the farm work and, when his chores were done, wandering through meadow, thicket and marsh, interested in the living growing things of nature. Northeastern Indiana is a lovely pastoral region, with attractive woodlands and many small lakes. Stimulated by this environment, the innate curiosity of an observant boy developed into a deep desire to know more about plants and animals. The collector's instinct appeared in him early, and he still treasured, in his later years, a herbarium prepared in his high school days. Even earlier he had accumulated and preserved wild flowers, insects, and fossils. In high school he was fortunate in having in Wallace Harsh a teacher of exceptional ability and understanding, who noted his interest in collecting and encouraged him to go further with his studies. After finishing high school he taught for two years in the local country schools and then, in the autumn of 1897, entered Wabash College at Crawfordsville, Indiana.

Herbert Hice Whetzel
(At about 35 years of age)

Toward the close of his freshman year trouble with his eyes caused him to return home. After staying out of college for a year, when he again taught school, he returned to Wabash in the autumn of 1899 and finished his course, graduating in 1902 with the A.B. degree.

Wabash is a small college of arts and sciences for men. At that period the student body numbered little more than two hundred. The staff consisted of about a dozen professors, all of them very able. In such a school the student is acquainted with most of his fellows and is in close contact with his professors. There Whetzel came under the influence of Professor Mason B. Thomas, an exceptionally successful teacher of botany. In a relatively short lifetime Thomas sent many of his men to the graduate schools of the universities, and saw a goodly number of them attain distinction in botany, bacteriology, forestry, medicine, and plant pathology. Reared in central New York State he had been trained in biology at Cornell, and had gone to Wabash College in 1891 as successor to John M. Coulter. He recognized in Whetzel a student of exceptional promise.

During his four undergraduate years Whetzel, inspired and guided by Thomas, prepared himself for a botanical career. He gained insight into various phases of botany, and seems to have shown early a preference for mycology. In his senior year he presented two small papers before the Indiana Academy of Science, one an experimental investigation of *Gymnosporangium Juniperi-virginianae* (1), the other a taxonomic study of the local species of *Stemonitis* (2). Throughout his life he retained a special interest in the rusts and slime moulds which dated back to those days of collecting around Crawfordsville.

Professor Thomas desired that Whetzel go for graduate work to Cornell, his own alma mater, and most fortunately obtained an assistantship for him there in the Department of Botany under Professor George F. Atkinson. Following his graduation Whetzel proceeded at once to Ithaca, and in early July was already enthusiastically collecting Agaricaceae, Boleti, and other fleshy fungi in the company of Professor Atkinson and C. H. Kauffman. The region about Ithaca with its varied topography and mixture of coniferous and hardwood forest provided in a season of good col-

lecting a rich and varied fungus flora such as Whetzel had not seen before. Throughout that summer he collected energetically by day, and pored over his specimens and the taxonomic literature by night. Years later at the death of Professor Atkinson he wrote in almost a poetic vein of their hours together in the field (**25**). He says: "With large market baskets on our arms we have wandered through the dark damp woods searching eagerly for the choice mushroom treasures that lifted their frail caps from leaf mold, mossy banks, decaying logs or soggy sphagnum. Joyfully we called to each other as we knelt over some rare or gorgeous find. How his eyes sparkled and how tenderly and deftly he lifted the lowly beauty from its place, turning it round before us to admire its slender form or rare coloring. How eagerly we listened to the comments and explanations about it drawn from his wonderful store of knowledge of the habits, haunts and peculiarities of his fungus friend."

At that period Professor Atkinson held the chair of botany in the University, and was also Botanist of the Agricultural Experiment Station. In the latter capacity in preceding years he had emphasized research on plant diseases and had written several well-known station bulletins including one on "Leaf Curl and Plum Pockets" and another on "Damping Off." Of late, however, he had shifted his interests more and more to the study of the mushrooms, and had adopted the policy of referring most of the station work on plant diseases to his assistants. Whetzel applied himself industriously to the problems assigned to him and in April, 1904, published his first station bulletin, bearing the title "Onion Blight" (**4**). It was based on his observations during the preceding season in the fields of commercial growers. He stated it to be a preliminary report, and undertook a more searching study of the disease and its causal organism as a thesis problem for the doctorate degree. In the late spring of 1904, he was promoted to an instructorship with responsibility for conducting most of the plant disease investigations. He remained in that status for two years and, in addition to assisting Professor Atkinson in teaching and research, had nearly completed the requirements of the Graduate School for the degree, when, in the summer of 1906 four years after his arrival at Cornell, he was appointed Assistant Professor of Botany

and head of another Department of Botany then being established by Dean Liberty Hyde Bailey in the newly organized State College of Agriculture. The next year, October 1, 1907, at his own request, his title was changed to Assistant Professor of Plant Pathology, and his department was designated the Department of Plant Pathology. As Dr. Bailey has recently said, "Whetzel broke easily with tradition" and as a result, in this instance, gained the distinction of founding the first department of plant pathology in the United States (Phytopathology **12**: 499). Having accepted appointment to a professorship, he was no longer eligible for his degree at Cornell, and it was never granted, but Wabash College conferred the honorary M.A. on him in 1906 and the honorary D.Sc. in 1931. He had received the honorary D.Sc. in 1926 also from the University of Puerto Rico.

In May, 1904, at his promotion to an instructorship, Whetzel went back to Avilla, Indiana, the home of his boyhood, and married Lucy E. Baker. Returning to Ithaca he spent eight happy years with her in Forest Home. In June, 1912, she was stricken by a baffling illness and died leaving two small children, Gertrude and Joseph, the younger only twenty months old. In the summer of 1914, while abroad on his first sabbatic leave, he married one of Lucy's younger sisters, Bertha A. Baker, in London. Returning home that autumn he began life anew. Twenty-five years later, December 25, 1939, Bertha preceded him in death. Lucy and Bertha were charming and capable women, both much beloved by the department group. Professor Whetzel is survived by his mother, a brother, three sisters, two children and four grandchildren.

Fate was kind, both to plant pathology and Whetzel, in bringing him to Cornell at the beginning of the period of greatest expansion the New York State College of Agriculture has enjoyed. During the decade following the establishment of his department the college appropriations were greatly increased, the staff was much enlarged, and nine of the twelve major buildings now on its campus were erected. He became a full professor at the end of two years, and his department grew rapidly. In the summer of 1907, Donald Reddick was appointed as its first instructor and, after obtaining his Ph.D. in 1909, also was advanced to a full professorship in

First Department of Plant Pathology in its Second Winter 1908–1909 The entire department group is shown in the south laboratory of the top floor of Stone Hall Cornell University Back row—Gertrude Whetzel H H Whetzel C N Jensen J J Taubenhaus M F Barrus Donald Reddick Front row—Mrs Lucy Whetzel Agnes McAllister Errett Wallace

1911. He too had been trained under Thomas and Atkinson. As Whetzel outlined expanding programs of research, teaching, and extension, more positions were made available, and other young men, chiefly from Wabash College, were added to the staff.

During the department's second year, in early January, 1909, the American Phytopathological Society was voted into being at Baltimore. Professor Whetzel and Dr. Reddick were present at that occasion, and both attended the first meeting of the Society the following winter at Boston. At the Boston meeting the Society completed its organization and elected Whetzel a member of its first council. The journal *Phytopathology* was established shortly thereafter. Its first number, printed in Ithaca, appeared in February, 1911, and Reddick was business manager during its first four years. Three editors, L. R. Jones, C. L. Shear, and H. H. Whetzel, with twelve associate editors, constituted the first editorial board. Whetzel served as editor for two years. Reddick passed from the status of business manager to that of editor in 1915, and functioned in that capacity until 1918. Whetzel became president of the Society in 1915, and, during the First World War, served energetically as chairman of its War Emergency Board directing an extensive campaign for improved methods of plant disease control. During the Society's early years the young Department of Plant Pathology at Cornell thus played a prominent and significant role.

Having started with a wholly new department unincumbered by antiquated equipment or impeding precedents, Whetzel showed a keen interest in the problems of organization confronting him and gave much time and thought to details of arrangement and procedure. In Atkinson's laboratories, and probably in those of most departments of biological science at that period, apparatus and materials intended for the general use of staff and graduate students were scattered over desk tops or on open shelves available to all. This lack of order resulted in loss of time and equipment most distasteful to Whetzel. He provided a store room; stocked it very completely, and ruled that staff members and students alike must sign check-out slips at its window. He placed one man in complete control of the department's photographic facilities and had him do all of its photography. Having been adversely im-

pressed by certain inadequacies in the customary method of mounting herbarium specimens of fungi on sheets in genus covers, Whetzel adopted a system in which uniform-sized packets are filed upright in cabinet drawers in numerical sequence without regard to the position of the organisms in the natural classification. Associated materials, such as photographic negatives and prints, slides, and notes, are filed similarly in numerical order in diverse cabinets designed for their respective needs. Accession cards, arranged alphabetically, enable even the most non-mycologically trained to consult the collections. In all such procedures Whetzel sought to provide the best possible working conditions for the entire department group, and though at times in his enthusiasm for organizing he promulgated regulations approaching regimentation his motives in so doing were not selfish, and the measures were designed always for the general good. The department owes its existence and some of its outstanding characteristics to his vision and untiring industry in its early years.

In 1909, confronted with many plant disease problems in New York State which could not be investigated for lack of funds, he committed the department to the then much questioned policy of seeking financial support directly from groups of growers and business organizations. He established "industrial fellowships" under the terms of which the department supplied laboratory equipment and supervision, while those hoping to benefit from the research provided the salary of an investigator (13). Each of these fellowships was adequate for the support of a graduate student for several years, and the research undertaken afforded him a thesis problem for the doctorate degree. Located during the growing seasons in a "field laboratory" in the midst of the growers, the fellow conducted his experiments under actual field conditions. The success which attended Professor Whetzel's efforts to obtain funds for the fellowships was phenomenal. In the aggregate they provided many thousands of dollars for endowment of research, increased the department staff, and advertised the institution widely and favorably. He traveled throughout the State, meeting the farmers and addressing their organizations, and at that early period became one of Cornell's best known extension men. He possessed to a pronounced degree the attributes of the success-

ful salesman, and he "sold plant pathology" enthusiastically to the Dean, the grower, and the general public. He kept in close contact with the research in progress in the department, and many of his short early articles on plant disease control represent his efforts to advertise the accomplishments of his students and make their results immediately available to the grower. His personal contribution to phytopathological research is scattered through numerous papers. Many of the investigations conducted by the students were outlined by him and developed under his direct supervision. Though he contributed freely by suggestion and criticism to their success he rarely shared in their publication. He had a contagious enthusiasm for investigational work that infected all who came in contact with him, and his driving energy stimulated the students and staff to increased endeavor.

In 1922, in the fifteenth year of the department's existence, he resigned as its head, and announced his intention to devote the rest of his life to teaching and research. He remained in charge of the elementary courses, while one of his younger colleagues, Dr. L. M. Massey, who had come as a student from Wabash College in 1912, succeeded him as head. Relieved of time-consuming executive duties, Professor Whetzel applied himself to the furtherance of various activities which he had reserved for his later days (Phytopathology **12**: 499).

Throughout his years in the university he had been regarded as an outstanding teacher. His courses had a high reputation among the students; he gave to them unstintingly of his time and energy; and he was a lucid and entertaining lecturer. Nevertheless, he became convinced that in following the methods of teaching in vogue in institutions of higher learning, he was failing to train students to think for themselves, and, after a period of planning and experimentation, he adopted for his elementary course in plant pathology a wholly new method of instruction in which lecturing plays a very minor role. Limited only slightly in his choice, the student selects for study those diseases for which he has a preference, and, the laboratories being open at all times, works at his own convenience, receiving aid from his instructors only when he himself seeks it. Having completed to his own satisfaction the study of one of the diseases, he presents himself

for an individual conference at which he must demonstrate not only a detailed knowledge of the disease, but also the ability to use his facts in the solution of problems, presented for his consideration, in which emphasis is placed on the general principles of plant pathology. This method of instruction is discussed in detail by Professor Whetzel in his article, "An Experiment in Teaching" (**37**). It has proved popular with the students and has given very satisfactory results. Though Whetzel was a teacher of exceptional native ability, his outstanding success in teaching may be said to have resulted in large part from his high evaluation of its importance. He did not subordinate his personal or departmental activities in teaching to those in research, and he looked with favor on the development of well-organized courses as an aid in training graduate students.

Professor Whetzel brought himself to the attention of the younger generation of plant pathologists nowhere more sharply perhaps than in his contributions to the terminology of their science. In his attempt to organize the subject matter of phytopathology for the purposes of teaching he had been impressed by the great need for radical revision of the terminology, and applied himself to the task. He defined the terms precisely, limiting some of the older widely-used ones to a narrower application than that in which they had previously served. Also he coined a number of new terms for concepts not covered with adequate exactness by the older terminology (**35**). Though he encountered resistance to these innovations he used the terms, as he defined them, in teaching and publication, and his students and many others are following in his footsteps to a considerable extent. Probably the future historian of phytopathology will regard Professor Whetzel as one of its great teachers and will emphasize in that connection that his insistence on clear thinking and precise expression was one of his most noteworthy contributions to his science. It must be conceded that in coining new terms, as in some other respects, he tended to be somewhat radical, and clearly took pleasure in nettling the ultraconservatives.

While engaged in his early studies of the diseases of ginseng and peony, Professor Whetzel encountered several species of *Botrytis* and *Sclerotinia* (**17, 18, 19**). Obtaining these in pure

culture he made a comparative study of their sclerotia, noting differences in size and shape that seemed to offer a basis for taxonomic separation. Also he became much interested in an early paper in which observations were recorded indicating that *Botrytis cinerea* is the conidial condition of *Sclerotinia Fuckeliana.* In 1913–1914, he spent fifteen months in Europe on sabbatic leave, and, though in residence at the University of Heidelberg during the winter studying plant physiology in the laboratory of Professor Georg Klebs, he found time during the growing seasons for travel and collecting. In the spring of 1914, he searched unsuccessfully on the Continent for apothecia of *S. Fuckeliana* and returned home frustrated in his plan to culture the species and settle the question of its possession of a *Botrytis* stage. A few years later he was especially gratified to be able to coöperate with G. H. Godfrey in demonstrating that *S. Ricini* does unquestionably have *Botrytis* as its conidial condition. These experiences mark the beginnings of his interest in *Sclerotinia.*

As the years passed Professor Whetzel gave an increasing amount of time to research on the genus, and by 1922, when he retired from the headship of the department, had decided to prepare a monograph of the North American species. Each year, thereafter, it was his custom to spend several weeks in the early spring in intensive collecting, searching painstakingly for developing apothecia. His success in finding them was extraordinary. At the time of collection he sought evidence as to their host relationships, and later from additional collections and inoculation experiments verified his assumptions. On his return to the laboratory he obtained each species in pure culture, usually from discharged ascospores. Aided by a succession of technical assistants, trained by him in his methods, he rapidly built up a large collection of cultures and herbarium specimens, accompanied by excellent photographs, drawings, and notes. Soon he had advanced further in the study of these fungi than any preceding investigator, and had available for study in pure culture a considerable number of species never before recorded. Becoming recognized as the authority on the group he received additional interesting material from collectors elsewhere and in 1930 spent eight months in Europe collecting and studying the previously described species of

England, Holland, France, Germany, and the Scandinavian countries in their type localities. Though students of the Discomycetes for the most part had been content to study only the apothecium, he emphasized that many species of *Sclerotinia* cannot be separated on apothecial characters alone. His diagnoses embrace information concerning conidial, spermatial, and sclerotial stages also, and emphasize cultural characters, as well as data on pathogenicity and life-history.

In 1926, he published the first of a series of monographic studies of individual species under the general title, "North American Species of *Sclerotinia*" (**30**). It was not long, however, until he came to realize, from encountering border-line conditions, that his field of investigation must be broadened to include the genus *Ciboria* and other related inoperculate Discomycetes in which the apothecium arises from a stroma or stromatized substratum. Also he became convinced that the taxonomic situation would be clarified by breaking up the older generic concepts into smaller subdivisions. He began calling his group the Ciborioideae, and, in addition to *Sclerotinia* and *Ciboria*, recognized as valid members—*Stromatinia* Boudier, *Monilinia* Honey, *Ovulinia* Weiss, *Lambertella* von Höhnel, and *Rutstroemia* Karsten as emended by Rehm and White. Also he established three new genera of his own, *Septotinia* (**42**), *Martinia* (**47**) and *Coprotinia* (**52**), and had in preparation for publication a paper in which he expected to erect five additional ones. During the last eighteen years of his life he wrote eleven taxonomic papers on the group (**30, 34, 41, 42, 44, 47, 49, 51, 52, 53, 57**). His last contribution entitled "The Cypericolous and Juncicolous species of *Sclerotinia*" embraces ten species and is expected to appear early in 1946 in *Farlowia*. In March 1943, he proposed the establishment of the new family Sclerotiniaceae (**49**: p. 18) and stated that he would shortly publish a characterization of the family with a synoptical treatment of its genera. This he failed to accomplish. Though he had written a portion of the paper and had prepared a table of contents in which he listed the fifteen genera that he proposed to include, his final illness prevented its completion. He entitled the paper "A Synopsis of the Genera and Species of the Sclerotiniaceae" and expected to condense into it many of his as yet unpub-

lished ideas on family limits, generic separations, comparative morphology, and terminology. He had begun its preparation with reluctance, feeling that such a synoptical presentation could not safely be given until monographic studies of all the genera had been completed. He was aware, however, of the critical condition of his health, and had begun to suspect that he might not live to complete the unfinished monographs.

Though Professor Whetzel in his earlier days had directed most of his investigations toward the solution of economically significant problems in plant pathology, his interests were always largely mycological, and his work on the Sclerotiniaceae during the last twenty-five years of his life was unquestionably his major accomplishment in research. To it he gave his best efforts, and out of it came probably his most noteworthy publications. It is especially to be regretted, therefore, that his untimely death prevented him from summarizing his accomplishments in this important group of fungi.[1]

His enthusiasm for field work was one of his well-known characteristics throughout his life. He collected in Puerto Rico with Dr. E. W. Olive for three months in 1916 (**21**), with Dr. F. D. Kern throughout the summer of 1924 (**28**, **29**, **31**) and with Carlos E. Chardon in the spring of 1931. He spent the year 1921–1922, on sabbatic leave, in Bermuda and, while acting as the first plant pathologist appointed to the Bermuda Department of Agriculture, found time to collect fungi intensively. He returned to the island in 1926 and, accompanied by Dr. F. J. Seaver and Lawrence Ogilvie, made additional collections (**32**, **33**). From the accumulated specimens he prepared the first century of the exsiccati set, Bermuda Fungi. One or more additional centuries are now being prepared, chiefly from these collections, by J. M. Waterston, the present plant pathologist of the island. Finally, in 1939, Whetzel spent three months in Venezuela collecting with Albert S. Müller and Carlos E. Chardon (**40**).

Professor Whetzel was a member of the committee of three, including also Dr. H. C. Cowles and Dr. B. M. Duggar, which

[1] After this memorial article had been submitted for publication, the writer undertook the task of finishing Professor Whetzel's manuscript. The paper is now nearing completion and will appear in an early number of MYCOLOGIA.

organized the International Congress of Plant Sciences (Fourth International Botanical Congress) that met at Ithaca, in August, 1926. He also acted as chairman of the committee on local arrangements and worked indefatigably for weeks to make the congress outstandingly pleasant and successful. The foreign visitors especially will remember his megaphone and his clarion voice sounding through the corridors of Willard Straight Hall as he announced events and gave instructions. Four years later he attended the meetings of the Fifth International Botanical Congress in Cambridge, England.

It has been indicated above that he was a charter member of the Mycological Society of America and the American Phytopathological Society and served as president of both organizations. He was also a member of the Botanical Society of America and the British Mycological Society. Until the last few years he had maintained membership in Société de Pathologie Végétale and Vereinigung für Angewandte Botanik. He was a fellow of the American Association for the Advancement of Science, and an honorary member of the Academy of Medicine of Des Moines, Iowa. He belonged to Phi Delta Theta, Gamma Alpha, Alpha Zeta, Phi Gamma Mu, Phi Kappa Phi, Phi Beta Kappa, and Sigma Xi. The highest local recognition accorded him was his election by the faculty of the whole university to a five-year term as one of their three representatives on its Board of Trustees.

In Ithaca he was widely known outside university circles, and his exceptional capacity for friendship made him one of Cornell's best liked professors. He thoroughly enjoyed his contacts with his fellow men, and conversation and argument meant much to him. He was a member of the Rotary Club and looked forward with anticipation to its weekly luncheon. He was not a sportsman. Games such as tennis or golf made no appeal to him and seemed at best a waste of time. In his hours of relaxation he experienced the greatest satisfaction in working with the soil. During the latter part of his life he developed his home flower garden of nearly an acre until it was one of the most interesting in the community. Though placing little emphasis on arrangement, he assembled many beautiful and unusual plants. His bed of trilliums embraced species from many regions, and he had specialized

in the genus *Sedum* until his plantings attracted even the taxonomist. His extensive and varied rock garden, containing at times as many as four hundred different species, was his special pride. He made a hobby of growing wild flowers from seed, some of them received from former students in distant lands (48). In recent summers he contributed occasional articles to the local newspaper in which he announced developments among his plants as the season advanced. The flower lovers of Ithaca were notified when some choice lily was in bloom or were urged to come and enjoy the garden with him at its best.

When this winter's heavy snows have melted away and his trilliums bloom again he will not be there to see. And at the university, in the years ahead, as his former students return, one by one, to visit the old department that holds so much for them of pleasant recollection, the absence of his hearty welcome will be keenly felt. He who was "Prof" to all of them is gone, not to return, but the deeply personal memory of his friendship, his tolerance, and his understanding will be with them as long as they shall live.

CORNELL UNIVERSITY,
ITHACA, NEW YORK

PUBLICATIONS

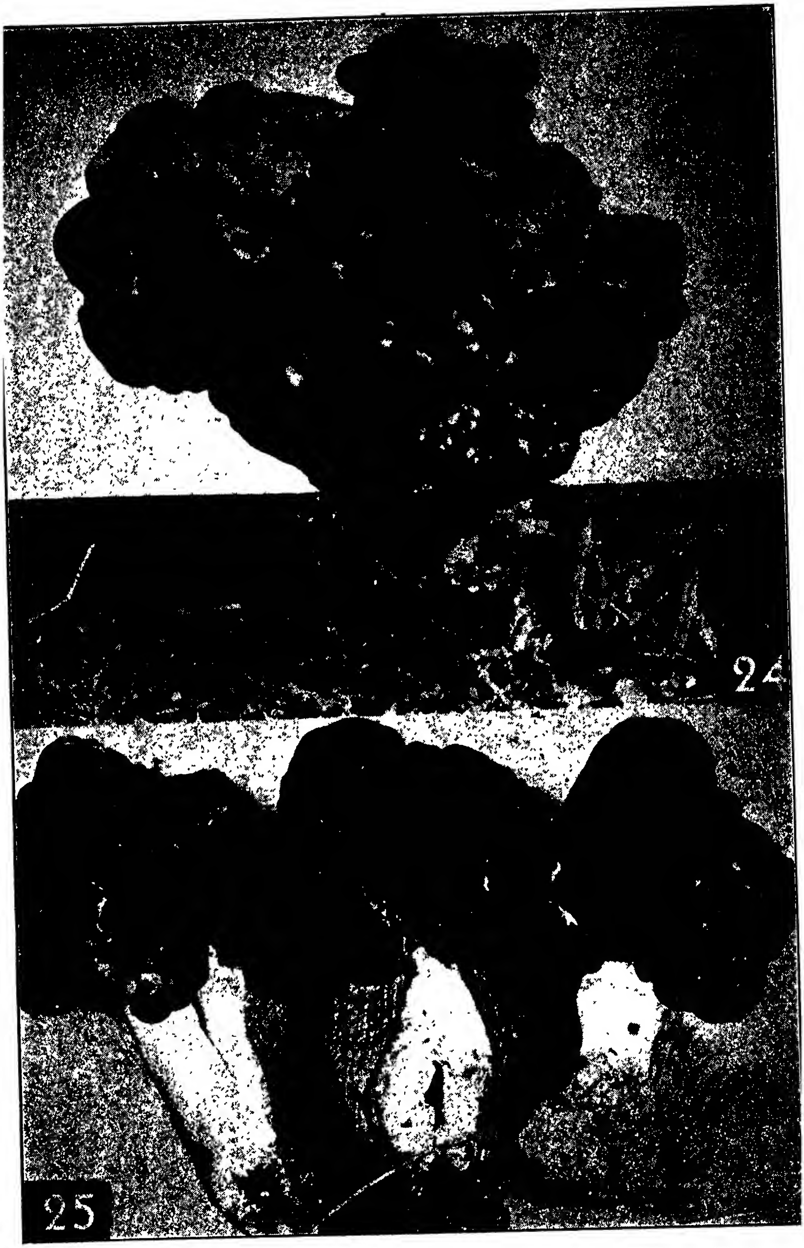
An approximately complete list of Professor Whetzel's publications will appear in *Phytopathology*. They number more than two hundred. Many of them deal exclusively with plant disease control, or are short phytopathological notes lacking mycological interest. The list below is believed to include all of his significant mycological contributions, as well as about a dozen papers on other subjects.

1. Notes on apple rusts. Indiana Acad. Sci. **1902**: 255–261.
2. Notes on the genus Stemonitis. Indiana Acad. Sci. **1902**: 261–266.
3. A new method of mounting superficial fungi. Jour. Mycol. **9**: 218–219. 1903.
4. Onion blight. N. Y. (Cornell) Agr. Exp. Sta. Bull. 218: 138–161, *figs. 1–17.* 1904.
5. The diseases of ginseng. Special Crops **4**: 170–171. 1905.
6. The Alternaria blight of ginseng. Cornell Countryman **4**: 33–41. 1906.
7. Some diseases of beans. N. Y. (Cornell) Agr. Exp. Sta. Bull. 239: 198–214, *figs. 100–115.* 1906.
8. A parasitic fungus that winters in the seed of its host. Ontario Nat. Sci. Bull. **4**: 7–9, *figs. 1–4.* 1908.

9. Bean anthracnose. N. Y. (Cornell) Agr. Exp. Sta. Bull. 255: 431–447, *figs. 217–222.* 1908.
10. A fungus living as a parasite upon another fungus. Ontario Nat. Sci. Bull. 5, *figs. 1–2.* 1909.
11. Grape rot. Proc. N. Y. State Fruit Growers' Assoc. **8**: 141–144. 1909.
12. (With Donald Reddick.) Occurrence of the aecidial stages of willow and poplar rusts in nature. Science **32**: 805–806. 1910.
13. The industrial fellowship in plant pathology. (Abst.) Phytopath. **1**: 68–69. 1911.
14. The local plant doctor. Trans. Mass. Hort. Soc. **1911**: 27–38.
15. (With Errett Wallace.) Apple scab. N. Y. State Dept. of Agr. Bull. *28*: *252–259.* 1911.
16. (With Donald Reddick.) A method of developing Claviceps. Phytopath. 1: 50–52, *pl. 11.* 1911.
17. (With Joseph Rosenbaum.) The diseases of ginseng and their control. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 250: 6–44, *pls. 1–11, figs. 1–5.* 1912.
18. Diseases of the peony. Trans. Mass. Hort. Soc. **1915**: Part 1: 103–112, *pls. 1–2.*
19. (With Joseph Rosenbaum, J. W. Braun, and J. A. McClintock.) Ginseng diseases and their control. U. S. Dept. Agr. Farmers' Bull. *736*: 1–*22, figs. 1–26.* 1916.
20. (With Lex R. Hesler, C. T. Gregory, and W. Howard Rankin.) Laboratory Outlines in Plant Pathology. pp. 1–207. Published by the authors, 1916. Revised edition pp. 9–231. W. B. Saunders Co., Philadelphia, Pa. 1925.
21. (With E. W. Olive.) Endophyllum-like rusts of Porto Rico. Amer. Jour. Bot. **1**: 44–52, *pls. 1–3.* 1917.
22. (With Lex R. Hesler.) Manual of Fruit Diseases. pp. 1–462, *figs. 1–126.* Macmillan Co., New York City. 1917.
23. An Outline of the History of Phytopathology. pp. 1–130. W. B. Saunders. Co., Philadelphia, Pa. 1918.
24. George Francis Atkinson. Bot. Gaz. **67**: 366–368. 1919.
25. George Francis Atkinson. The Guide to Nature 12: 70–72. 1919.
26. (With John M. Arthur.) The gray bulb-rot of tulips caused by Rhizoctonia tuliparum (Klebh.) n. comb. N. Y. (Cornell) Agr. Exp. Sta. Memoir 89: 3–18, *figs. 1–8, pls. I–VII.* 1925.
27. (With H. S. Jackson and E. B. Mains.) The composite life history of Puccinia podophylli Schw. Jour. Agr. Res. **30**: 65–79, *pls. 1–3.* 1925.
28. (With F. D. Kern.) Some new and interesting Porto Rican rusts. Mycologia **18**: 39–47. 1926.
29. (With F. D. Kern.) The smuts of Porto Rico and the Virgin Islands. Mycologia **18**: 114–124, *pl. 16.* 1926.
30. North American species of Sclerotinia—I. Mycologia **18**: 224–235, *pls. 27–29, fig. 1.* 1926.
31. (With F. D. Kern.) Hemibasidiomycetes. Ustilaginales and Uredinales. Scientific Survey of Porto Rico and the Virgin Islands. Botany of Porto Rico and the Virgin Islands. *In* Fred J. Seaver

and Carlos E. Chardon. Mycology. New York Academy of Sci. **8**: 1: 107–144. 1926.
32. (With F. J. Seaver and Cynthia Westcott.) Studies on Bermuda Fungi I—Poronia leporina. Mycologia **19**: 43–50, *figs. 1–5, pl. 5.* 1927.
33. (With H. S. Jackson.) The rusts and smuts of Bermuda. Trans. British Mycol. Soc. **13**: 1–32. 1928.
34. North American species of Sclerotinia—II. Two species on Carex, S. duriaeana (Tul.) Rehm., and S. longisclerotialis n. sp. Mycologia **21**: 5–32, *fig. 1, pls. 1–5.* 1929.
35. The terminology of phytopathology. Proc. International Congress Plant Science **2**: 1204–1215. 1929.
36. (With F. D. Kern.) Uredinales. *In* C. E. Chardon and R. A. Toro. Mycological Explorations of Colombia. Jour. Dept. Agr. Porto Rico **14**: 301–348. 1930.
37. An experiment in teaching. Scientific Monthly **31**: 151–162, 1930.
38. (With F. L. Drayton.) A new species of Botrytis on rhizomatous iris. Mycologia **24**: 469–476, *pls. 15–16.* 1932.
39. (With F. D. Kern and H. W. Thurston, Jr.) Annotated index of the rusts of Colombia. Mycologia **25**: 448–503. 1933.
40. (With F. D. Kern and H. W. Thurston, Jr.) Uredinales. *In* Carlos Chardon and Rafael A. Toro. Mycological Explorations of Venezuela. Monographs of the University of Puerto Rico—Series B, No. 2: 262–303. 1934.
41. (With N. Fabritius Buchwald.) North American species of Sclerotinia and related genera. III. Ciboria acerina. Mycologia **28**: 514–527. 1936.
42. Septotinia, a new genus of the Ciborioideae.. Mycologia **29**: 128–146. 1937.
43. (With W. Lawrence White.) Pleomorphic life cycles in a new genus of the Helotiaceae. Mycologia **30**: 187–203. 1938.
44. Sclerotinia bifrons. Mycologia **32**: 124–127. 1940.
45. (With W. Lawrence White.) Mollisia tetrica, Peziza sejournei and the genera Phaeociboria and Pycnopeziza. Mycologia **32**: 609–620. 1940.
46. Ciliospora albida. Mycologia **34**: 525–531. 1942.
47. A new genus and new species of brown-spored inoperculate Discomycetes from Panama. Mycologia **34**: 584–591. 1942.
48. Growing wild flowers from seed. Journal New York Botanical Garden **43**: 244–247. 1942. (Illustrated by a photograph showing Professor Whetzel in his garden.)
49. A monograph of Lambertella, a genus of brown-spored inoperculate Discomycetes. Lloydia **6**: 18–52. 1943.
50. The spermodochidium, an unusual type of spermatial fruitbody in the Ascomycetes. Mycologia **35**: 335–338. 1943.
51. (With W. G. Solheim.) Sclerotinia caricis-ampullaceae, a remarkable sub-arctic species. Mycologia **35**: 385–398. 1943.
52. A new genus of the Sclerotiniaceae. Farlowia **1**: 483–487. 1944.
53. Saccardo's confusion of the spermatial stage of S. duriaeana and S. curreyana with the Sphacelia stage of Claviceps nigricans. Mycologia **36**: 426–428. 1944.

54. (With J. M. Waterston and J. W. Sinden.) Notes on the Geoglossaceae of Bermuda. Mycologia **37**: *32–36, 1 fig.* 1945.
55. (With F. A. Wolf.) A cup-fungus, Ciboria carunculoides, pathogenic on mulberry fruits. Mycologia **37**: , 1945. (In press.)
56. A synopsis of the genera and species of the Sclerotiniaceae, a family of stromatic inoperculate Discomycetes. Mycologia **37**: , 1945. (In press.)
57. The cypericolous and juncicolous species of Sclerotinia. Farlowia **2**: No. 3, Jan. 1946. (In press.)



Gyromitra esculenta.

SOME WESTERN DISCOMYCETES GYROMITRA ESCULENTA, HELVELLA LACUNOSA

Elizabeth Eaton Morse

(with 25 figures)

Gyromitra esculenta Fries, 1849 [1]

(= *H. esculenta* Pers., 1800) Elias Magnus Fries erected a new genus *Gyromitra* to include those *Helvellae* which have gyrose or brain-like folds in the caps. The two illustrations shown in the frontispiece are believed to be fairly typical of material such as Fries met. In each there is a rather smooth, stout stem at the summit of which is produced an erect, compact head, inflated, knob-like or brain-like in aspect, bearing the hymenium. The two illustrations are quite different, but Fries' brief description applies equally well to each: "pileo inflato difformi undulato gyroso-rugoso brunneo, margine stipiti levi villoso adnexo."

Figure 24 grew in a cold, wet canyon, in disintegrated granite and soil in the lee of a huge log on the northwest slope of Mount Baker, Washington, was photographed and collected by W. T. Shaw, Fresno, California, July 20, 1926. Figure 25 grew in sandy soil in Pacific Grove, Calif., Feb. 24, 1914, N. L. Gardner, collector.

A fine specimen of this species up to eight inches in stature, weighing nearly one pound, was collected by J. Dearness, Ontario, Canada, which he sent to the National Museum of Canada at Ottawa. He reports unfavorably on the edibility of this species, since two fatalities from eating this fungus were investigated by him. Louis C. C. Krieger published this species as "deadly poisonous"; he reported 160 deaths (see Mushroom Handbook, p. 326, 1936). There is a possibility that what we are calling *G. esculenta* is not identical with the European *esculenta*.

[1] See Fries, Syst. Myc. 2: 16, 17, 607. 1823.

G. esculenta is considered one of the rarest of the large western Discomycetes, in fact the writer knows of no examples other than those shown in the frontispiece which may be claimed to fit into this species as understood.

Whether or not *Gyromitra* should be given full generic rank or be regarded as a variation of *Helvella* is a favorite topic for discussion among mycologists! That *Gyromitra* macroscopically and microscopically is very close to *Helvella* cannot be denied. A structural distinction may be claimed which would secure for *Gyromitra* a standing among genera. Our contact with these gyrose forms is too meager to form an unshaken opinion. On this point, Doctor Dearness writes that he considers that "*Gyromitra* is in the literatures to stay."

For Saccardo's treatment of the four genera *Verpa, Helvella, Gyromitra, Morchella* in equal rank, see his key (Syll. Fung. **8**: 7. 1889).

Of the ten species listed as Gyromitras by Saccardo six of them had been described as species of *Helvella* (Sacc. Syll. Fung. **8**: 15–17, 1889).

HELVELLA LACUNOSA AFZEL. 1783

(= *Elvela Mitra* Linnaeus, 1753)

Helvella lacunosa is a well-known and widely distributed discomycete which has been described and illustrated repeatedly by botanists in many European countries, in Canada and in the United States. It is an exceedingly variable species in stature, form, coloration and general aspect. In all localities with the exception of the Pacific Slope an estimate of average stature is 6–7 cm. Specimens in the region of Seattle, Washington, have reached 20 cm. in height (Stuntz), in Berkeley 16 cm. (Morse), and in Santa Barbara 18 cm., and cap 5–10 cm. broad (P. M. Rea). Thus far the range is from Santa Barbara, California to Pitt Island on the coast of British Columbia, found in deep moss, under *Thuja plicata,* rainfall approximately 100 inches (McCabe); doubtless this range will be extended both north and south.

The main purpose of this article is to present variations which occur in this western area. These variations may be attributed

wholly or in part to great humidity and to the mild two-season climate of the Pacific Slope.

My favorite collecting ground is a steep hillside planted to *Pinus radiata* and *P. edulis,* overlooking the stadium of the University of California in Berkeley with the Golden Gate in the distance. Specimens arise in dense colonies from soil beneath a carpet of rotting coniferous duff. They appear during and following the heavy rains in the autumn and winter months, with temperature about 60 to 70 degrees. The steep hillside is significant, because it affords excellent drainage and helps to prevent the decay of fungous tissue.

The description which follows is based upon the observation and study of a large amount of material, both fresh and dried, and may be considered composite.

HELVELLA LACUNOSA AFZEL

Pileus—up to 9.5 cm. wide, blackish from the first, brittle, wax-like in texture, mitrate, inflated, variously folded and contorted, borne on ribs which are extensions of the cortex of stipe, turns back on, or is attached to, the stipe at several points, grayish on under side.

Stipe—up to 20 cm. long by 3.5 cm. wide, snow-white at first, later becomes smoke-gray, wax-like in aspect but cartilaginous, often labyrinthine throughout (FIG. 7), passages often closed making pockets, or opening to the exterior showing slit-like apertures of great variability; may be fairly slender, equal, or ventricose and narrowed to base, or much enlarged at base (FIG. 4); cross sections of stipes show honeycomb aspect of empty lacunae (no liquid) (FIG. 7); stipes may be very wide (FIG. 10), or two stipes may be completely coalesced (FIG. 8), or partly so, or merely attached at bases by mycelium; abundant mycelium may bind gravel and soil into solid masses, at base of stipes, usually left by collectors in the forest duff (FIGS. 12, 16, 17; also Mycologia **35**: 574–5, *figs. 10, 11*).

Asci—cylindric, gradually narrowed to base, around 275 × 15 μ, 8-spored (FIG. 23).

Spores—ellipsoid, hyaline, smooth, containing one large oil-drop, 19–22.5 × 12.5 μ, uniseriate.

Paraphyses—septate, slightly enlarged at tips.

A structural distinction in the arrangement of the fertile tissues of *Gyromitra esculenta* and *Helvella lacunosa* may be claimed: as

previously stated, *Gyromitra* makes a definite, erect, compact head on a stem stout enough to support it, while *Helvella* grows a cap with lobed margins which turn back on the stem to which it is usually attached at intervals.

There may be a crumpling of the fertile tissues of the cap which suggests relationship to *Gyromitra*, but no specimens ever extend beyond the crumpled stage; furthermore, the peculiar distinctive lacunose stipe which characterizes this species holds these larger specimens in this series (FIGS. 6, 7, 8, 9, 10, 11).

Various types of lacunose stipes are met in *Gyromitra*, but we are not aware of any like these shown in our illustrations of *Helvellae*. I consider the *Gyromitrae* shown in the frontispiece distinctive and unlike all my other collections.

ANTIQUITY OF THE NAME HELVELLA

Referring to the voluminous notes supplied me by J. Dearness, we find that the word *Helvella* may have come from a Greek word allied to our "edible" in meaning. If the Greek spelling begins with " the syllable is aspirated, *e.g.* *h*-e-l-v; if it begins with ", the syllable is smooth. Greek dictionaries place both forms in the same column. The first letter of a word is important in indexing.

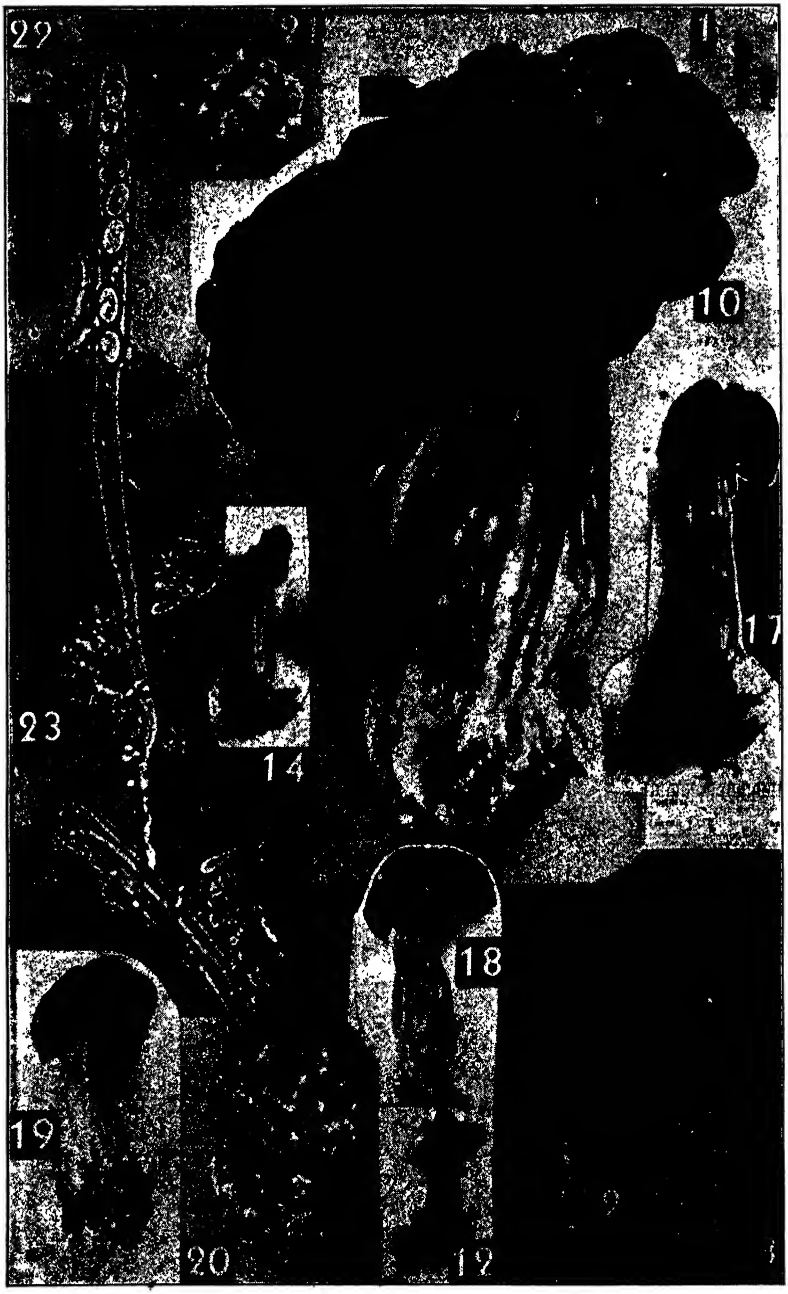
Cicero, born 106 B.C., died 43 B.C., and other Latin authors, used the word *Helvella*, applying it to a kind of fungus.

Coming to the time of Linnaeus, he, in 1753, appropriated the name for a genus, spelling it *Elvela;* however, he changed that spelling two years later to read *Elvella*. Eight years later, in 1763, in his second edition of Species Plantarum he described *Helvella Mitra,* implying a choice and decision of spelling which we are adopting.

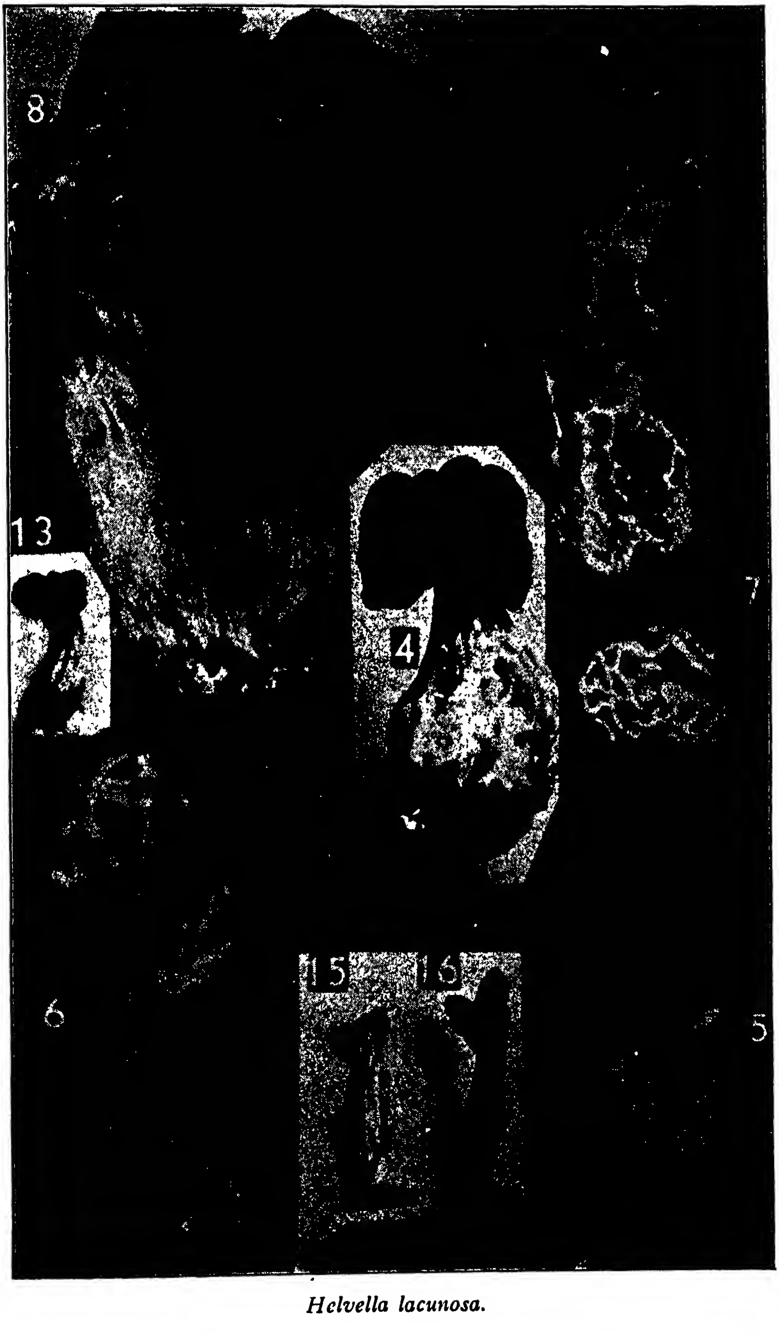
In regard to the use of "Mitra" as a species name, Dr. J. C. Loudon, a good Latin scholar, in 1865 states that "Mitra" has been applied to so many species that it, *Mitra,* has been abandoned altogether. Many expert mycologists have referred *H. Mitra* to synonymy of *H. lacunosa*. Dr. Seaver in the additions to his monumental work[2] states that *"Mitra"* should be replaced by *"lacunosa"* Afz.

[2] *The North American Cup-Fungi (Operculates)*, 1942.

Helvella lacunosa



Helvella lacunosa.



Helvella lacunosa.

Adam Afzel was a pupil of Linnaeus at the University of Upsala. He described *Helvella lacunosa* in 1783; this name was accepted by Fries forty years later, and thus both the genus and species names became "legal," and in accord with the International Rules of Nomenclature.

FRIES' DESCRIPTION OF HELVELLA LACUNOSA

Syst. Myc. 2: 15. 1823: "pileo inflato lobato, cinereo-nigro, lobis deflexis adnatis; stipite fistuloso, costato-lacunoso."

We are not inclined to apply his varieties "major" and "minor" to our material, since he describes larger plants as having white stems, and smaller with smoky stems. All our specimens have stems more or less "smoky," according to climatic conditions. The transition from small to large is gradual, and no dividing line can be set. Also, we do not use var. *fumosa* Ellis & Ev. (North Am. Fungi *3039*. 1896) because smokiness of the stipe had been noted by Fries. At least six other varieties in addition to the above have been described by authors. These are merely speculative, as far as I know. I would not use them.

EDIBILITY OF H. LACUNOSA

Several authors claim edibility as a feature of this species. Odell, associate of Gussow, Canadian mycologist, was interested in fungi mainly from the standpoint of esculence; he states: "fried in butter, they make a delicious dish." Collector Perona, Sausalito, California, eats this species, but he does not find it uniformly desirable from season to season. Most authors are silent on this point.

DISCHARGE OF SPORES WITH AUDIBLE SOUND [3]

If several specimens of ripe *H. lacunosa* are placed in a container, *e.g.* a shoebox, for several hours, and the cover then removed, the currents of air cause the lids of asci to fly up and millions of spores are released at the same moment. The discharge is accompanied by a distinct, suppressed, hissing sound. This is not an isolated experience with us. See A. H. Reginald

[3] For a popular account see The Whispering Fungus, Nature Magazine, August 1934, p. 84.

Buller, Researches in Fungi, Vol. I, p. 258, for discharge of spores in *Peziza Acetabulum* and *Helvella crispa;* also De Bary, Comparative Morphology and Physiology of Fungi, 1887, p. 92.

ASSOCIATION WITH TRICHOLOMA SCLEROTOIDEUM MORSE

Mycologie **35**: 573–581. 1943

There is no more recent report to make. Doctor Dearness hopes the question of relationship will yet be answered, and closes with the query: is the association accidental, symbiotic, or parasitic to the *Tricholoma* and to the *Helvella?*

It is my personal opinion that the strange, cheese-like growths out of which the agaric arises, in some way not understood, originate from the mycelium of the abundant *Helvella lacunosa* growing on the same hillside.

Doctor Dearness has been making studies on *H. lacunosa* since 1917, in Swedish, Swiss, German, French and English literatures, and has supplied these to me together with tracings from colored and black and white plates, microscopic measurements, and personal impressions. I am wishing to make grateful acknowledgments to him, to Doctors Lee Bonar and F. J. Seaver, as also to our technical assistant, Mrs. V. P. Miller.

CALIFORNIA MYCOLOGICAL SOCIETY,
UNIVERSITY OF CALIFORNIA,
BERKELEY, CALIFORNIA,
FEBRUARY 1, 1945

EXPLANATION OF FIGURES

Photomicrograph and photographs by W. C. Matthews and Victor Duran unless otherwise stated.

Helvella lacunosa Afzel.

Fig. **1–11**, **20–22** (× 1, or slightly reduced) (Morse). All caps black, all stipes lacunose, more or less "smoky." Fig. **1**, young ascophore, cap and stem differentiated; **2**, fully formed, cap lobed, free, stem equal, lacunose, orifices pronounced; **3**, cap saddle-shaped, stem enlarged at base; **4**, stem much enlarged at base, cap mitrate, margin lobed, free; **5**, a transitional form, cap expanded, shows *Gyromitra* aspect; **6**, cap contorted, lobed, two lobes turned up show grayish under-surface; **7**, vertical median section shows structure in attachment of cap to stipe, cap turns down on sides of stem (*Gyromitra* makes a head at summit of stem), lacunae branch and coalesce, often open to exterior; cross section shows lacunae vary in size and shape, dry; **8**, two stems completely coalesced or one broad stem branched

at summit; pale area at left cap shows ochre coloration; **9**,[4] a perfect, typical, well balanced specimen, attains the "high-water mark" of this species; cap lobed, free as in figure **4**; white spores lodged in depressions of cap; smokiness of stem is confined to the epiderm; stem fluted, orifices large (cross section from another specimen); **10**, also a prize specimen, "stocky," cap lobed, convolutions not far removed from some *Gyromitrae;* **11**, cap, saddle-shaped to lobed (Fig. **3**), grown to stipe on under side, somewhat convoluted, but never attains the brain-like aspect of *G. esculenta;* shows the maximum stature in this series.

Fig. **12–17** (× ½), Richardson collection, Eureka, California, Swanlund studios; **12**, **13**, **14**, **15**, **16**, caps saddle-shaped; **15**, attacked by mold, *Mycogone cervina* (determined Cash, Washington, D. C.); **17**, cap mitrate, lobed, attached at intervals to stipe.

Fig. **18**, **19**, from Setchell-Gardner collections, Marin Co., also Pacific Grove, Calif. Caps mitrate, free, convoluted, stems typically lacunose; reduced.

Fig. **20**, **21**, **22**, solid, basal masses of soil and gravel bound firmly by mycelium (no "cheese"), not readily broken apart. (See Mycologia **35**: 574, 575, figs. 10, 11, 1943.) See scale in margin.

Fig. **23**, photomicrograph of ascus (280 μ, J.D.), narrowed below, lodged against another ascus, eight spores towards the tip, walls smooth, each spore containing one large oil-drop.

CONCLUSION: I am inclined to think that large forms such as I show at figures **6**, **7**, **8**, **9**, **10**, **11** may not have been met often by other collectors. Doubtless Schaeffer (1774) had large forms, for he described a variety "major" (Sacc. **8**: 19).

We have here in the west many notable examples of giant forms in other species of fungi. It appears that *Helvella lacunosa* extends that list.

[4] For a companion specimen, see Textbook of general botany, Holman and Robbins, fig. 307, p. 411, 1934.

NEW AND INTERESTING SPECIES OF BASIDIOMYCETES

R. Singer

(with 1 figure)

The following notes are intended to present new facts on various groups of Basidiomycetes, especially Agaricales. It is, no doubt, preferable to treat the taxonomic groups separately and monographically, but in many instances, the information available is either too incomplete to be combined into monographic studies, or comes merely as a more detailed supplement to be added to existing monographs. If such scattered information were withheld, the progress of taxonomic mycology would indeed be much slower. This first series of new and interesting species is concerned mainly with material from Florida.

I. A NEW SPECIES OF CLAVARIA

Clavaria floridana Sing. sp. nov.

Carpophoris caespitosissimis sed vix base connatis quamquam saepe fasciculariter crescentibus, simplicibus vel bifurcatis in parte inferiore vel saepius in parte superiore, rarissime ramosis, saepissime compressis vel canaliculatis, apice acuto et parte superiore fertili cinerea (in vivis), exsiccando atrocinerea instructo, parte inferiore abrupte delimitata, albo-flavida, tenuiore quam pars superior fertilis, 50–80 × 2–5 mm., intus albis, carnosis, moderate fragilibus, inodoris, mitibus. In dumetis tropicalibus ad terram.—Sporis levibus, 7–8.5 × 5.8–7.5 μ; cystidiis et fibulis nullis; basidiis bisporis.

Carpophores very cespitose (from afar sometimes like a gray turf) but the bases not connate though often fasciculate, simple or forked below or more often above, rarely almost crested as in *Clavulina cristata*, very rarely 2- to 6-branched, very frequently compressed, or canaliculate, with acute tips, the larger upper fertile part cinereous when fresh, dark cinereous when dried, the lower part sterile, yellowish white or whitish yellow, yellowish when dried, the fertile and the sterile parts very abruptly and distinctly delimited, mostly about 2–3 mm. broad in the fertile part, rarely up to 5 mm. in diameter, 50–65 mm. high, more rarely up to 80

mm. high; context white, fleshy, moderately fragile, solid, inodorous and mild to the taste. Spores 7–8.5 × 5.8–7.5 μ, subhyaline, subglobose or very shortly ellipsoid, with a large central oil-drop, non-amyloid, smooth; basidia 38–42 × 6.7–7.5 μ, 2-spored; cystidia none; trama hyaline, subregular, but the hyphae strongly interwoven, very variable in size and shape, short to long, attenuate at the septa or equal, 2–15 μ in diameter, thin-walled; clamp connections none; pigment a membrana-pigment, olive, brownish-melleous in alkalis.

Habitat: In tropical hammocks, usually on the ground or occasionally on small rotten sticks or leaves, fruiting in summer and fall, Dade Co., Fla. (type collection *R. Singer F 733*, preserved at the Farlow Herbarium).

This is not like any of the northern species. It reminds one remotely of *Clavaria cinereoatra* Rick from Brazil which, however, has larger spores (in our specimens, they are 8.5–10.3 × 7.5–8.8 μ). The distinction between *Clavulina* and *Clavaria* as pointed out by Donk seems rather satisfactory on paper but the more species are examined the more obscure it becomes. Even the cytological distinction is uncertain since only a minority of the species have been studied in this regard. In my experience, the typical *Clavulinae* have clamp-bearing septa. This would tend to exclude *C. floridana* from the genus *Clavulina*, and its basidia may be expected to be chiastic.

II. A LACTARIUS WITH YELLOW, WATERY LATEX

Lactarius xanthydrorheus Sing. sp. nov.

Pileo isabellino, magis brunneolo discum versus vel centro intensius colorato vel colore *Marasmii floridani* Murr. gaudente, marginem versus saepe ad olivaceum vergente, margine saepe subsulcato-subcrenato, centro plerumque distincte rugoso-venoso, subglabro, subplano, margine deflexo, disco papillato, dein omnino plano (papilla neglecta), demum concavo, 9–25 mm. lato; cuticula structura *Russulae virescentis* gaudente.—Lamellis cremeis, subdistantibus, arcuato-decurrentibus in tertia interiore, latiusculis; sporis in cumulo cremeo-albis; sub microscopio 8.7–10 × 7.5–8.7 μ, cystidiis sparsis.—Stipite lamellis concolori versus apicem, media in parte lamellis vel pileo concolori, ad basin albido, solido, dein cavo, subglabro, levi, 11–22 × 3 mm.—Carne alba vel albida, fragili, miti, inodora; latice aquoso, pellucido, luteo. In silvis et dumetis humidis.

Pileus "Isabella color," sometimes more brownish on the papilla, or deeper and richer colored in the center, or approaching the color of *Marasmius floridanus* Murr. (this color cannot be matched

in the color charts), often tending to olive on the margin (*pl. 15, L 12*, or *pl. 14, L 9*, Maerz & Paul), often short-sulcate and almost crenate at the margin, the center usually conspicuously rugose-venose, rarely less conspicuously so, subglabrous, almost flat with initially convex-deflexed margin and papillate center, very rarely an occasional individual without papilla, the papilla persistent in age, even in the last concave stage, 9–25 mm. broad.—Lamellae cremeous (*pl. 9, C 2, M. & P.*), subdistant, *i.e.* 19–27 through-lamellae present, subventricose near the margin and arcuate-decurrent behind, rather broad (about 5 mm.); spore print creamy white (between A and B of Crawshay).—Stipe at the apex concolorous with the lamellae, in the middle also concolorous with the lamellae or concolorous with the pileus, at base whitish from a tomentose mycelioid coating, subglabrous, smooth, solid, sooner or later becoming hollow, mostly subequal, 11–22 mm. long and about 3 mm. broad.—Context of the pileus white, of the stipe sordid white, fragile in all parts; odor none; taste mild. Latex not milky, watery and transparent, yellow.

Microscopical characters: Spores 8.7–10 × 7.5–8.7 μ, short-ellipsoid to subglobose, echinate, asymmetrical, hyaline, ornamentation 1–1.8 μ high, consisting of spines or short ridges, connected by low veins forming a complete or incomplete network (type IIIa, IIIb, or II, few IV, V, VI); basidia 42–49 × 9–10.5 μ, clavate, 4-spored; cystidia about 55 × 7.5 μ, very few, without banded contents, subfusoid-clavate, hyaline; cuticle of the pileus consisting of chains of spherocysts (8.5–23 μ in diameter) with filamentous terminal appendages, the latter forming the epicutis, 22–25 × 4–7 μ, sometimes not separated from the last spherocyst by a septum, and then the last member bottle-shaped, all these elements filled with a brownish-fuscous cell-sap; all septa without clamp-connections.

Chemical characters: **KOH** on surface of pileus, negative; with latex "primulin yellow" to "light cadmium" (*i.e* more intensely yellow).—**NH_3, NH_4OH, HNO_3** on surface of pileus, negative.—**$FeSO_4$** on surface of pileus, negative; on context "normal" (*i.e.* reddish gray).—**Phenol** deep chocolate.—**Methylparamidophenol** on context indistinctly reacting, strongly positive only with the edges of the lamellae.

Habitat: In dense low hammocks, especially when intermixed with *Pinus palustris*, on the soil, along the trails, on very decayed stumps, among *Sphagnum* or other mosses, or among pine needles; gregarious. Fruiting in July and August.

Distribution: Florida.

The type (*R. Singer, F 134*) from Highlands Hammock State Park, and co-types from there as well as from the Sugarfoot Hammock, Alachua Co., Fla., is preserved at the Farlow Herbarium. This species belongs in the section *Plinthogali* Burl. because of the structure of the cuticle, but it is most unusual in regard of the latex. The latter is possibly at first hyaline but changes to yellow so fast that the hyaline stage cannot be observed.

III. A NEW SPECIES OF RUSSULA (FIG. 1)

Russula ferrotincta Sing. sp. nov.

Pileo, albo, pallide lilaceo tincto vel pallide lilaceo et albo-maculato, maculis ferrugineis minutissimis saepe asperso, cuticula sicca, subvelutina vel velutina margineque obtuso, at haud rotundato, levi praedito, convexo, applanato centroque depresso in vetustis, 50–131 mm. lato; epicute corpusculis laticiferis destituta, crinibus microscopicis obsita.—Lamellis candidis, interdum fractis brunnescentibus, aequalibus vel nonnullis brevioribus intermixtis, angustis, anguste adnexis, subconfertis vel confertissimis; sporis in cumulo albis; sporis 7–8 × 5.5–5.8 μ, verrucis venulis subconnexis, 0.2–0.3 μ altis obtectis; cystidiis sulphovanillini ope caerulescentibus.—Stipite candido, subtiliter pruinoso, e solido farcto, aequali vel basin versus attenuato, 45–132 × 15–34 mm.—Carne alba; odore nullo; sapore miti; $FeSO_4$ varie reagente, solutione phenolica lilascente. In silvis sub quercubus, vernalis.

Pileus white with more or less extensive "light purplish vinaceous" or "pale purplish vinaceous," more rarely "pale brownish vinaceous" areas which eventually become more or less "brownish drab," sometimes with this lilac tinge occupying the larger part of the pileus while in other caps not a trace of it is seen, but most caps in between these extremes, with the lilac color more often concentrated near the margin than otherwise, dry, subvelutinous to velutinous, less velutinous toward the center, frequently faintly rivulose, often cracking rimosely on the disc, opaque, often with some rutsy spots or dots, especially near the margin, convex, then with depressed center, the marginal half eventually becoming flat, with the margin itself always obtuse but not rounded (subobtuse), smooth, only in some very old and large specimens eventually sulcate, 50–131 mm. broad, usually 75–95 mm. broad.—Lamellae white, sometimes stained brown where wounded, a few or many forked, with very few to many lamellulae, not broad (4–5 mm.), or sometimes broader in caps of more than 100 mm. diameter, not ventricose, subclose to crowded, broadest in the marginal third, rather flexible (less so than in *R. cyanoxantha*) to moderately brittle, narrowly adnexed, often with decurrent tooth; spore print pure white (A in Crawshay).—Stipe pure white, exceptionally

with a "pale purplish vinaceous" hue at the apex (but probably from pigment washed off the cuticle of the pileus), finely pruinose all over, solid and firm, becoming spongiose and fragile with age, equal or tapering downwards, 45–132 × 15–34 mm.—Context white, rather firm at least initially, odor none; taste mild.

FIG. 1 *Russula ferrotincta.*

Microscopical characters: Spores (from print) 7–8 × 5.5–5.8 μ, ellipsoid, or nearly subglobose, hyaline, warty, ornamentation of type IIIb or IV, rarely V (*i.e.* warts connected by a few to many thin lines which may form an incomplete network), 0.2–0.3 μ high; basidia 34–44 × 8.7–10.2 μ, 4-spored; cystidia 35–58 × 7.8–10 μ, versiform, mostly clavate-subfusoid, bluing at least in the upper half in sulphovanilline; trama with rather numerous spherocysts; epicutis of the pileus consisting of erect hyaline, non-incrusted hairs; hairs capitate, clavate, ventricose below or in the middle and then ampullaceous above, etc., (8)–20–50 ×4.5–7.5 μ, forming a palisade; the basal hyphae of these hairs erect or ascendant, usually short, narrowed at the septa (thus sometimes approaching the shape of a spherocyst), forming short chains which constitute the subcutis.

Chemical characters: **KOH** negative.—**$FeSO_4$** on surface of pileus, gray to slate violet or greenish (to "dark olive buff"), surprisingly variable in different collections but always positive and in the above colors; on context of stipe salmoneous or salmoneous-pallid, or greenish in the cortex, gray in the cottony interior (very variable); on lamellae green or yellowish cinnamon with a salmoneous tinge, or salmon color.—**Sulphovanilline** negative or merely blue with some purplish when applied in fresh condition; when applied in dried condition, it causes no reaction or a deep blue one in the cottony interior of the stipe, and a bluish black and carmine one in the cortex, or becoming "garnet brown" all over.—**H_2SO_4** on surface of pileus, duller flesh color (reaching color of *R. vesca*), then bleaching to white.—**Phenol** in cottony interior of stipe "normal" (to chocolate color), but in cortex "deep brownish vinaceous," "russet vinaceous," "sorghum brown," eventually deep chestnut with the cortex remaining as above.—**Methylparamidophenol** positive (violet), moderately strong and moderately fast reaction.

Habitat: In high hammocks with *Quercus virginiana* on the ground, in small groups.

Distribution: In and around Gainesville, Alachua Co., Florida, U. S. A.

The type is preserved in the Farlow Herbarium (*F 1889 a*); other collections (*F 1889, F 1889 b, F 1889 c, F 1889 d, F 2103, 2103 a*) are co-types. Our figure 1 is based on additional material collected later in June.

This species reminds one somewhat of *R. cyanoxantha* but it has at least a subvelutinous pileus, not to mention the anatomical and chemical differences. It belongs in the section Rigidae where it is somewhat intermediate between the Lilacea-group of the subsection Lepidinae and the Vesca-group of the subsection Chlorinae. I have compared all of Murrill's types at Gainesville but neither the specimens nor their descriptions of any fit this new species. It reminds one most of the northern *R. flocculosa* Burl. The type of the latter has been examined by the writer (Mycologia **34**: 75. 1942) and found to be similar to *R. vesca* in many regards, especially as far as the structure of the epicutis is concerned. It is precisely the structure of this layer of the cuticle that makes it safe to assume that *R. ferrotincta* is different from *R. flocculosa* because the hairs of the latter are much narrower as compared

with the basal cells, and more filamentous. Also, the lamellae are subdistant in *R. flocculosa* instead of close.

IV. REDESCRIPTION OF RUSSULA PULVERULENTA PECK

Pileus between "drab" and "buffy brown," nearer to the latter in most cases, or with more pale buff or grayish pallid throughout, initially pulverulent all over with a loose mealy velar covering and fine isolated flocculae around the margin, this veil about "amber yellow" and easily rubbed off the cuticle proper (never innate), the pileus becoming glabrescent after strong rains and in age and then much like *Russula pectiata,* minutely radiately rugulose, somewhat viscid after rains, with separable cuticle (excepting the depressed part of the pileus), with a 6–10 mm. broad marginal zone strongly pectinate-sulcate at maturity, with acute margin, subsemiglobose and often somewhat umbilicate, becoming convex and usually depressed in the center, eventually often concave, 42–80 mm. broad.—Lamellae white to whitish, eventually pale cream color, rather narrow to medium broad (3.5–8 mm.), attenuate-free, close to medium close, not ventricose, anastomosing or not, forked at the stipe, equal or irregularly intermixed, simple or with many forked ones intermixed, broadest in the middle; spore print pale cream color (B or Crawshay).—Stipe white, somewhat fulvous-yellow or yellow on the base (from veil), glabrous to subglabrous, subrugulose, equal or subfusoid, soft, soon becoming hollow, 25–54 × 8–20 mm.—Context white, often somewhat sordid-gray under the cuticle of the pileus, rather fragile, at least when old; taste submild but somewhat disagreeable to acrid, its acridity up to moderate; odor oily (like that of *R. foetens* but lacking the almond or nitro-benzine element), but weak.

Microscopical characters: Spores, basidia, cystidia, and cuticular elements see in my analysis of Kauffman's material (Bull. Soc. Myc. Fr. **55**: 230. 1939). The cuticle is not visibly divided into an epicutis and a subcutis, the epicutis proper being reduced to occasional hair-like terminal members of the subcuticular hyphae; the veil, if examined in fresh material (otherwise it is almost impossible to find it and examine it separately), consists of slender, tender, elongate, cylindric-filamentous, smooth hyphae with cylindric terminal members, with rounded tip, with thin walls, clampless septa, hyaline to ochraceous (in NH_4OH) cell-sap and 2.5–3.5 μ diameter; neither the veil nor the cuticle proper contain elements bluing in sulfovanilline, even when fresh.

Chemical characters: **KOH** with the vein on the pileus and on the base of the stipe immediately and characteristically "Mars orange"; with the cuticle slightly darkening; on context somewhat

vitreous-hyaline-gray.—**HNO_3** on veil and cuticle, negative.—**$FeSO_4$** on context, pale reddish gray (dirty salmoneous with some yellowish gray mixed in), so-called "normal" reaction.—**Chlorovanilline** negative, eventually becoming blue.—**Phenol** on context, fast rather rapidly changing to chocolate color.—**Methylaparamidophenol:** quickly and strongly dark violet in all parts.

Habitat: In hammocks, mixed and frondose forests, on shaded lawns and in gardens, on earth or on decayed wood (*e.g. Liquidambar styraciflua*) or on the base of frondose trunks (*e.g. Persea*), most frequently found in the neighborhood of oaks but by no means exclusively with *Quercus*.[1] Mostly solitary or in small groups; fruiting from May until November in Florida, comparatively shorter fruiting periods are observed farther north.

Distribution: From New England west to Michigan and south to the southern tip of Florida and along the Gulf Coast, becoming increasingly common toward the south.

Several interesting conclusions can be made from the above data. The veil is the same as in *R. subvelata* Sing. from the Caucasus, type species of the section Subvelatae, and, except for a slight difference in color, in *R. mutabilis* Murr. from Florida. This veil has the same appearance and anatomical structure as in the pulverulent boletes (*Pulveroboletus Ravenelii* and *P. subacidus*). *R. pulverulenta* differs from *R. subvelata* chiefly in the not white (A) but pale cream (B) spore color, the either disagreeable or acrid taste and oily odor (though both odor and taste are rather weak), the slightly stronger development of the velar layer in the center of the pileus in an average of young specimens, and perhaps the slightly smaller number of hair-ends in cuticular hyphae. While *R. pulverulenta* prefers oaks, though often growing independent of them, *R. subvelata* seems to prefer *Carpinus*, yet sometimes is found far from them. The taste is occasionally mild in *R. pulverulenta*, and then the two species may be rather similar in their external characters. Peck's type is the same species that we have collected and described above. However, Beardslee's *R. pulverulenta* is definitely something else. We had difficulties in finding the proper position of this species in the classification

[1] In one case we collected it with *Pithecolobium* and fruit trees around it but all the usual mycrorrhizal trees completely absent.

mainly because of this difference in interpretation in the American literature. We thought that it may possibly belong in the section Subvelatae (Bull. Soc. Myc. Fr. **51**: 303. 1935) but later transferred it to the Ingratae (Bull. Soc. Myc. Fr. **55**: 230. 1939). Both these sections are more closely related to each other than to any other sections of *Russula*, yet, as far as *R. pulverulenta* is concerned, it turns out that our first guess was right.

V. A NEW SECTION AND A NEW SPECIES OF TRICHOLOMA

While discussing certain types of species belonging to *Tricholoma* and allied groups (Lloydia **5**: 111–117. 1942), we have, in a sketchy way, outlined our classification of the tricholomas proper. This new classification can be expressed in the following key:

A. Clamp connections present; surface of the pileus not sericeous; odor not of gas tar or lilac flowers...........Subgenus **Contextocutis** Sing. nom. nov. (*Rigida* Fr. *sensu orig.*)
  B. Pigmentless species................Section *Leuco-Rigida* Sing. *ined.*
  B. Pigmented species.
    C. Spores nearly evenly ellipsoid to ovoid.....Section *Rigida* Fr. em.
    C. Spores subangular, crest-shaped, etc.......Section *Io-Rigida* Sing.
A. Clamp connections rarely present, and then the pileus at least subsericeous, whitish, and with odor of gas tar or lilac flowers.
Subgenus *Eu-Tricholoma* Lange, em.
  D. Hyphae of the cuticle of the pileus subparallel, never gelatinized; pileus sericeous or subglabrous with initially fibrillose-velutinous margin; odor of gas tar or lilac flowers, more rarely absent.
Sect. *Sericella* Fr. em.
  D. Hyphae strictly parallel at least in the upper layer of the cuticle, or if somewhat wavy, distinctly imbedded in a gelatinous mass; pileus viscid and then often glabrous or innately fibrillose, or dry and then mostly distinctly tomentose to squamose, not sericeous.
    E. Pileus gray, umber, whitish with gray fibrils, or golden lemon yellow; lamellae white, yellowish, gray, or pink, not rusty-spotted.
Sect. *Limacina* Fr. em.
    E. Pileus cinnamon, buff, orange yellow, orange red, rufous-brown; lamellae white, buffy pallid, pallid, light yellow, often with rusty spots, especially when old..................Sect. *Genuina* Fr. em.

The section *Io-Rigida* Sing.[2] consists of several interesting and rare species one of which does not seem to have ever been de-

[2] *Tricholoma,* subgen. **Contextocutis** nom. nov. (= sect. *Rigida* Fr. *Tricholomate saponaceo* Fr. typo), sect. **Io-Rigida** Sing. sect. nov. Sporis subangulatis vel cruciformibus; hyphis fibuligeris; pigmento saepe lilascente vel purpurascente. Species typica: *Tricholoma pseudosordidum* Sing.

scribed before, and which is proposed as a new species of *Tricholoma.*

Tricholoma pseudosordidum sp. nov.

Pileo purpureo-violascente, haud hygrophano, tenui, levi, glabro, 24 mm. lato; lamellis concoloribus, confertis, adnexis et subrotundatis 3.7–5.5 × 3–4.8 μ, inamyloideis, hyalinis, admodum asymmetricis, cruciformibus; cystidiis nullis; basidiis granulis carminophilis destitutis; stipite concolori, innate subfibrilloso, excentrico, deorsum incrassato, 30 × 5 mm.; carne subconcolori, ex hyphis fibuligeris consistente; odore saporeque haud notabilibus. Inter folia in dumeto tropico in Florida.

Pileus "litho purple" or "Saccardo's violet," slightly more sordid in the middle, non-hygrophanous, smooth, glabrous, thin, subumbonate-flat, about 24 mm. broad—Lamellae concolorous but appearing somewhat paler because of a hyaline pruinosity (spores ?), rather broad, subventricose, close to crowded, narrowly adnexed and somewhat rounded.—Stipe concolorous, with faint, hyaline, innate fibrils, and therefore appearing lighter colored than the pileus, eccentric, or irregularly compressed, tapering upwards, about 30 × 5 mm.—Context subconcolorous, non-hygrophanous; odor and taste not distinctive.

Microscopical characters: Spores 3.7–5.5 × 3–4.8 μ, mostly 4–5 × 3–4 μ, hyaline, non-amyloid, smooth, very asymmetric, *viz.* short ellipsoid with a suprahilar depression or applanation and a papilla on the opposite side when seen in profile, but when seen frontally there are two such papillae on both sides of the hilar end which is elongated between them like a projecting cone while the apex of the spores is gradually narrowed to an obtusely rounded tip, the frontal outline thus strongly cross-shaped, the central oil-drop also subangular; basidia 24 × 5.3–6 μ, without carminophilous granulosity, clavate, 4-spored; cystidia none seen; cheilocystidia (mucronate) and pseudoparaphyses (basidiomorphous) scattered at the edge of the lamellae, the size of the basidia, very inconspicuous; trama regular, of thin, somewhat interwoven, hyaline hyphae; epicutis of very interwoven, irregularly filiform, or swollen to clavate hyphae which are mostly repent, only occasionally suberect, thin-walled, very dilutely violet-blue inside (in NH_4OH), subcutis of thicker-walled (but moderately so) hyaline hyphae; all hyphae with clamp connections.

Habitat: In tropical hammock, among fallen leaves of *Ficus, Nectandra,* etc. on the ground, in the Coastal Hammock region near Miami, Dade Co., Florida. The type has been collected by R. Singer (*F 900*) in the Matheson Hammock, and is preserved at the Farlow Herbarium. It fruits in September.

Other species of this section have been described as *Tricholoma goniospermum* Bres., *Tricholoma Cossonianum* R. Maire, and *Tricholoma porphyrophyllum* Imai. Like some of these, *T. pseudosordidum* is similar to *Lepista sordida* in fresh condition. It will be taken for this latter species by the unsuspecting collector.

VI. A "FALSE" CRINIPELLIS

Marasmius Magnoliae Sing. sp. nov.

Pileo intense atrobrunneo, dein ferrugineo-fusco, intersticiis radialibus pallide alautaceo-tinctis, disco maturo crinito-ursino, margine maturo sulcato-rimoso, sicco, margine juniore fimbriatò-ciliato, disco 1.5 mm. lato, toto pileo usque ad 5.5 mm. lato, semiglobato, dein plano-convexo, centro subumbilicato, demum subapplanato centro subdepresso frequenter papillato in depressione; crinibus e catenulis hypharum vesiculosarum vel clavatarum, parte libera echinatarum, castanearum, crasso-tunicatarum consistente; lamellis albis, subliberis, distantibus, aequalibus, moderate latis; sporis 8.7–9.3 × 3.5–4.3 μ, hyalinis, non-amyloideis, levibus, ellipsoideo-fusoideis; cystidiis nullis; cheilocystidiis fusoideis, acutis, hyalinis, levibus, integris; stipite atrobrunneo, opaco vel rarius subnitido, ad apicem subattenuato, macroscopice subglabro, insiticio, flexuoso, 10–40 × 0.2–0.5 mm.; carne albida, exigua, ex hyphis tenuitunicatis, inamyloideis, fibuligeris consistente; odore nullo. In petiolis foliorum delapsorum *Magnoliae grandiflorae*, Gainesville, Fla.

Pileus deep brown, then "amber brown" with the depressions of the radiately sulcate-rimose margin pale buff, eventually somewhat pallescent and the margin as a whole about "clay color," hairy ursinous when mature, eventually somewhat glabrescent, the non-sulcate disk about 0.5 mm. broad, the extreme margin fimbriate-ciliate at first, hemispheric then convex, flattened at last and becoming subumbilicate, finally with a slight depression in the center in the middle of which there may be a small papilla, up to 5.5 mm. broad.—Lamellae white, subfree, distant, entire and equal, moderately broad (1 mm.).—Stipe blackish brown, macroscopically subglabrous but at least partially subfibrillose when seen under a lens, opaque, rarely slightly shining, insititious, more or less flexuous, slightly tapering at the apex, 10–40 × 0.2–0.5 mm.—Context white, whitish, very thin, inodorous.

Microscopical characters: Spores 8.7–9.3 × 3.5–4.3 μ, mostly 8.8–9 × 4–4.2 μ, hyaline, smooth, ellipsoid-fusoid, thin-walled, nonamyloid; basidia 26 × 6 μ; cystidia none seen; cheilocystidia about 4–7 μ thick, fusoid, acute, hyaline, smooth, entire; hairs of the pileus consisting of chains of short, vesiculose hyphae which are beset with brown, subpyramidal or cylindric spines of 2.5 μ length; among these hairs there are half-attached epicuticular hyphae which have the shape of ascendant claviculae, arising from each

other's lower side, or forming a chain of normal filamentous hyphae, rarely the hairs consisting of smooth members of free, erect hyphae-chains; these individual hyphae in all cases cited about 11–40 × 7–17 μ, the shortest ones *e.g.* 27 × 23 μ, all thick-walled; hyphae of the context hyaline, non-amyloid, filamentous, with clamp connections.

Habitat: On the petioles of fallen leaves of *Magnolia grandiflora,* very rarely on other parts of the tree, very gregarious in bay heads, fruiting only in May.

This is an interesting species and quite common in North Florida. The type has been collected at Gainesville by the writer and is preserved at the Farlow Herbarium. It has probably been overlooked by other collectors because of its small size, dark color, and unusually limited time of fruting, also because it is often covered by newly fallen leaves of neighboring trees. Macroscopically, it strongly suggests *Crinipellis.* Only the anatomical analysis reveals its affinity with *Marasmius.* In this latter genus, it belongs to the section *Hygrometrici* Kühner, a section in which we have indicated several species with a distinct specialization in regard to their host (*M. rotalis* Berk. = *M. hygrometricus; M. Buxi* Quél., *M. capillipes* Sacc., *M. Hudsonii* (Pers.) Fr., *M. aciculaeformis* B. & C., and others).

VII. THE TROPICAL SPECIES OF OUDEMANSIELLA

In *Oudemansiella,* two species are restricted to the tropics and subtropics. One of them has been named and renamed 30 times, the other not at all.

OUDEMANSIELLA CANARII (Jungh.) Hoehnel, Sitz.-ber. Akad. Wiss. Wien **118**: 276. 1909.

Agaricus Canarii Jungh. Batav. Genootsch. kunst. wetensch. Batav. Verhandl. **17**: [82]. 1838.

Amanitopsis Canarii Sacc. Syll. Fung. **5**: 27. 1887.

Agaricus alphitophyllus Berk. & Curt. Proc. Am. Acad. **4**: 112. 1860.

Mycena alphitophylla Sacc. l.c., p. 305.

Collybia alphitophylla Ito & Imai, Trans. Sapp. Nat. Hist. Soc. **16**: 15. 1939.

Agaricus leucoconis Berk. & Curt. l.c., p. 113.

Mycena leucoconis Sacc. l.c., p. 273.

Agaricus rhodoconis Berk. & Curt. l.c., p. 113.

Agaricus apalosarcus Berk. & Br. Jour. Linn. Soc. Bot. **11**: 520. 1871.
Collybia hapalosarca Sacc. l.c., p. 230.
Agaricus euphyllus Berk. & Br. l.c., p. 520.
Collybia euphylla Sacc. l.c., p. 229.
Agaricus magisterium Berk. & Br. l.c., p. 520.
Collybia Magisterium Sacc. l.c., p. 230.
Agaricus cubensis, Berk. & Curt. Jour. Linn. Soc. Bot. **10**: 282. 1869.
Amanitopsis cubensis Sacc. l.c., p. 25.
Agaricus cheimonophyllus Berk. & Curt. l.c., p. 284.
Armillaria cheimonophylla Sacc. l.c., p. 86.
Agaricus platensis Speg. Ann. Soc. Cient. Arg. **9**: 161. 1880.
Oudemansia platensis Speg. Ann. Soc. Cient. Arg. **10**: 280. 1880.
Oudemansiella platensis Speg. Ann. Soc. Cient. Arg. **12**: 24. 1881.
Oudemansiella apalosarca Hoehnel, Sitz.-ber. Akad. Wiss. Wien **117**: 1003. 1908.
Oudemansiella cheimonophylla Hoehn. Sitz.-ber. Akad. Wiss. Wien **119**: 885. 1910.
Mucidula cheimonophylla Pat. Bull. Soc. Myc. Fr. **15**: 192. 1899.
Mucidula alphitophylla Pat. Bull. Soc. Myc. Fr. **25**: 9. 1911.
Chamaemyces alphitophylla Murr. Mycologia **3**: 91. 1911.
Armillaria alphitophylla Murr. N. Am. Flora **10**: 39. 1914.
Phaeolimacium bulbosum Henn. Monsunia p. 14. 1899.
Pluteus macrosporus Henn. l.c., p. 57.

Pileus initially brownish or rarely hyaline, then very pale grayish brown to hyaline, covered with sordid elastic patches which recall the volva fragments of *Amanita*, these patches sometimes beset with scattered white flocculae, especially at the margin where they form an appendiculate veil, cuticle hygrophanous and at the same time glutinous, but eventually becoming dry, usually transparently striate (one tenth to three quarters of the radius), convex, eventually flattened, 12–92 mm. broad.—Lamellae white, thick at the ground (about 1 mm.) when mature, initially appearing fold-like because of a membranaceous or glutinous, sometimes collariately separating covering, ventricose and broad (3–13 mm.) when mature, tridymous, broadly adnexed or sinuate, the edges sometimes splitting longitudinally; spore print pure white, copious.—Stipe grayish hyaline to white, with a pure white pubescent or flocculose covering above the annulus, flocculose-squamulose below it (or where it should be), dry, solid, bulbous below, tapering up-

wards or downwards, or subequal above the bulb, the latter tapering into an indistinct fleshy-fibrose proliferation within the substratum, 10–65 × 2–11 mm.; annulus obsolete, narrow, or replaced by a more or less belt-like line of floccons around the lower part of the stipe, or sometimes entirely wanting.—Context white, fleshy; odor none; taste mild.

Microscopical characters: Spores 14–23 × 14–19 μ, hyaline, with or without irregular contents, with initially thick (1.5 μ), later thin or thick, smooth and non-amyloid wall and a little projecting asymmetrically attached hilar appendage, globose, without germinative pore; basidia 67–88 × 15.5–22 μ, clavate or slightly attenuate in the upper fifth, constantly with 4 broad-based sterigmata; cystidia sparse to very numerous, ventricose in the middle or below, thin-walled or with thickened walls in the broadest part, always broadly rounded above, sometimes capitate, hyaline, smooth and entire, with or without large, longitudinally elongate vacuoles, 75–180 × 19–30 μ; trama non-amyloid, of somewhat irregularly arranged hyphae but generally regular (not bilateral); marginal (partial) veil made up of subparallel, thin filamentous, hyaline hyphae, 1.5–7 μ in diameter; floccons on the patches of the pileus showing a similar texture; the sordid patches of the pileus themselves consisting of partly melleous to olive brown pigmented tissue of mixed spherocyst-chains and filamentous hyphae (reminding one of the heteromerous structure of some Asterogastraceae, the Russulaceae, and the cuticle of *Smithiomyces mexicanus* (Murr.) Sing.); cuticle pseudoparenchymatous; all hyphae without clamp connections.

Chemical characters: **Methylparamidophenol** on margin of pileus, on lamellae, and on context becoming "dull Indian purple," then "dull lavender," less distinctly positive on the rest of the carpophore.—**Phenol** on context weakly but distinctly chocolate.—**$FeSO_4$** negative.

Habitat: On living trunks, in old wounds, from 0–6 feet and even higher above the ground, also on old roots, and on freshly fallen trunks which are not thoroughly decayed, thus far observed on *Bursera simaruba*, *Canarium commune*, *Coccolobis laurifolia*, *Carya megacarpa*, *Ficus aurea* and *F. elastica*, *Liquidambar styraciflua*, *Nectandra coriacea*, *Quercus virginiana*, and on various grape vines [8] fruiting from May until October in Florida, and in accordance with the climate, practically around the year.

[8] This host list is based on observations by the writer in Florida (as is the whole description) with the single exception of *Canarium conmune* which is given by Junghuhn. This list obviously needs additional data from other areas.

Distribution: Pantropical, in this hemisphere from Florida south to Argentina.

Oudemansiella echinosperma Sing. sp. nov.

Pileo crenato-sulcato, fuscidulo-fuligineo, glabro; lamellis albis, subconfertis, latis, sinuosis; sporis 17–22 × 16–20 μ, echinatis; basidiis cystidiisque giganteis; stipite fuscidulo, subaequali vel bulbum basalem versus incrassato, pseudorhiza praedito; carne alba; magnitudine carpophorarum formas varias *Oudemansiellae radicatae* in mentem revocante. Sao Leopoldo, Rio Grande do Sul, Brazil.

This species is macroscopically very similar to *O. radicata;* the short macroscopical description deriving from notes and from dried material offers little evidence as for its separability from that species. However, the microscopical characters most certainly prove it to be an autonomous species. The spores are 17–22 × 16–20 μ, hyaline, non-amyloid, globose, and *beset by about 38–42 subcylindric to subpyramidal, hyaline spines,* projecting 1.8–3.2 μ and of about the same diameter at their base; basidia 43 × 16.5 μ (sterigmata not seen); cystidia fusoid to subcylindric, subcapitate, often with a resinous incrustation on top, the apex rounded, the walls thin, 100–160 × 9.5–30 μ, mostly 128–130 × 28–30 μ; epicutis formed by 15–32 μ thick globose cells with fuscous plaques of pigment, forming a continuous hymenial layer, connected with a stipe-like chain of cylindric erect or suberect hyphae, rooting in the context of the pileus and forming a sort of a subcutis; clamps not seen.

The type is based on a collection by J. Rick, deposited at the Farlow Herbarium under the name of *Collybia napipes,* and commented on in Broteria **6**: 72. 1907. When Hoehnel studied this specimen and compared it with the Kew types of *Collybia napipes,* he found out that the latter was a different species. He thought, however, as can be seen in notes in his herbarium, that Rick's plant was not different from *O. radicata.* This opinion can not be maintained in view of the echinate spores. Among the Marasmoideae, we now know echinate or stellate spores in two genera (*Marasmius nigripes,* the only *Marasmius* with stellate spores—*Marasmius cyatheae* being not a *Marasmius* but a *Mycenella,* most of which have echinate-warty spores); Marasmioid representatives of other white spored groups with echinate spores are *Laccaria. Lyophyllum tylicolor* (Fr. sensu Lange), and *Fayodia bisphaerigena* (Lange) Kühner. We are now adding *Oudemansiella echinosperma.*

VOLVARIA BOMBYCINA

Alexander H. Smith

(with 1 figure)

Volvaria bombycina (Fries) Quél. Champ. Jura Vosg. p. 114 (80). 1872.

Agaricus bombycinus Fries, Syst. Myc. 1: 277. 1821.

Volvariopsis bombycina Murrill, Mycologia 3: 281. 1911.

Pileus (5) 7–12 (20) cm. broad, more or less egg-shaped in the button stages, expanding to campanulate or convex, broadly convex to nearly plane at times in age, surface dry and silky fibrillose or in age becoming somewhat squamulose, rather coarsely fibrillose toward the more or less fimbriate margin, white, finally discoloring slightly to yellowish on the disc, when dried more or less "cinnamon buff" at least on the disc; flesh rather thin, white, soft, mild, odor not distinctive; lamellae free and usually remote, broad and ventricose, crowded, white becoming flesh color from the spores, edges eroded; stipe 6–12 (20) cm. long, 1–2 cm. thick at the apex, solid, somewhat bulbous or merely tapering upward, often curved, white and glabrous, base inserted in the cup formed by the volva; volva thick, membranous, with the upper margin lobed or ragged, surface usually areolate from the checking of the outer layer, whitish at first but soon discoloring to sordid yellowish or near "Isabella color" on the areolae, merely sordid brownish when dried.

Spores pinkish in deposits, 7–8.4 × 5–6 μ, ovoid to ellipsoid, smooth, the walls slightly thickened; basidia four-spored, 28–34 × 7–9 μ, clavate but broadest about 6–10 μ below the apex, projecting 5–10 μ when sporulating; pleurocystidia fairly abundant, variable in size, 34–62 × (9) 12–18 (20) μ, thin walled, smooth, colorless in KOH, more or less fusoid ventricose, the apex drawn out to a subacute proliferation in some, in others merely obtuse; cheilocystidia very abundant, 38–56 (64) × 12–20 μ, ventricose or somewhat ellipsoid, the apex usually drawn out to an abrupt hair-like projection 10–18 × 4–5 μ; gill trama apparently inverse but not reviving well; pileus trama floccose, the fibrils on the surface more or less radially arranged, no clamp connections seen.

Volvaria bombycina

Usually solitary on decaying wood. Sometimes projecting from knotholes in living trees of maple, beech, elm, etc. It is widely distributed throughout central and eastern United States.

The accompanying photograph was taken by Mr. W. R. Fisher, photographer for the Department of Plant Pathology, Cornell University, Ithaca, N. Y. The specimens were collected in the vicinity of Ithaca by Mr. S. H. Burnham, June 30, 1942, and a portion of the collection and the photographs were sent to me for examination by Prof. H. M. Fitzpatrick. The microscopic characters given in the foregoing description were taken from this collection. In all the material of this species which I have examined the spores measured 6.5–8 × 5–6 μ. Some authors such as Ricken have given slightly larger spore measurements, 8.5–10 × 5–6 μ.

The fruiting bodies of this fungus are very beautiful and attract attention wherever found. Although it is widely distributed and supposedly not rare, I have never had the pleasure of collecting fresh specimens. Fresh material collected here in Ann Arbor and brought in by other collectors, however, has been examined. The fungus has been found rather frequently in the vicinity of Ithaca, New York (nos. *3096; 5340; 8114; 14,821* and *15,308* in the Atkinson Herbarium and nos. *262; 1996; 31,411; 22,851; 22,902; 31,737* in the Plant Path. Herbarium of Cornell University). An interesting story has been brought to my attention in regard to this species. The year before our entrance into the first world war the members of a family here in Ann Arbor were poisoned, some fatally, as the result of eating caps of a species of Amanita. The next year *Volvaria bombycina* fruited on a maple tree at the home of these people, and the story was circulated that some of the spores of the poisonous fungus, which caused the deaths the year before, had escaped from the house, lodged in the tree, germinated, grew and were now producing fruiting bodies. Consequently the carpophores of the *Volvaria* were held in great awe by the neighbors, and soon came to be referred to as the "ghost mushroom." No one, of course, would even consider eating them. This incident appears to me to be worth relating because it illustrates very well how the accidental occurrence of

a fungus may give rise to a superstition, and such a superstition once established is very difficult to dispel. *V. bombycina,* of course, is an edible fungus easily distinguished from the species of Amanita.

UNIVERSITY OF MICHIGAN,
ANN ARBOR, MICH.

FLAGELLAR STUDIES ON ZOOSPORES OF SOME MEMBERS OF THE MYCETOZOA, PLASMODIOPHORALES, AND CHYTRIDIALES [1]

Bernard R. Ellison

(with 4 figures)

INTRODUCTION

Since the discovery by Vlk (19, 20) that there is more than one type of flagellar structure, mycologists have been increasingly interested in the possibility that the type, position, number, etc., of the flagella might provide a valuable aid in classification and determination of phylogenetic relationships (3, 22). This idea is supported by the fact that there has been found to be a definite correlation between these flagellar characteristics and certain physiological and structural characteristics. This is true for both the fungi and the algae. It was with the hope of providing some information that could be used as an aid in determining the position and phylogeny of certain organisms of more or less uncertain relationships that these studies were undertaken.

Vlk's work disclosed that there are three different types of flagella. These are the ordinary, blunt-ended type of flagellum, the whiplash flagellum and the ciliated or "tinsel" type of flagellum. To these may be added a possible fourth type of flagellum, the knobbed flagellum. The occurrence and significance of the knobbed flagellum will be discussed in detail farther on in this paper.

Certain botanists tend to use the terms flagellum and cilium interchangeably. It is the author's opinion that this should be avoided in view of the fact that the term cilium, when used in

[1] This is a condensation of a portion of the thesis presented by the author in partial fulfilment of the requirements for the degree of Master of Science at Michigan State College.

reference to the swimming organelle of a unicellular organism, is well entrenched in zoological literature as referring to those distinctive structures (morphologically quite different from flagella) found on members of the Subphylum Ciliophora, Phylum Protozoa. A flagellum, as contrasted to a cilium, is that relatively long, whip-like, swimming organelle, characterized by having an outer sheath surrounding an inner core. The inner core arises typically from a blepharoplast which is in turn connected to the nucleus by a rhizoplast. It is in this sense that the terms flagellum and cilium are used in this paper.

MATERIALS AND METHODS

Planocytes were obtained both from material collected by myself and from material supplied by other collectors. It would be out of place in this paper to go into detail on the generalities of inducing the production and liberation of the planocytes in various organisms as there are a number of comprehensive articles on this subject (**10**, **11**, **13**, **18**, **21**). In the author's experience, however, there are no generalized methods which are effective in inducing production of the swarm spores. Each species, indeed each specimen, must be treated as an individual and zoospore production must be induced by a laborious process of trial and error. Robert Hagelstein in a letter to the author expressed the opinion that germination studies based on individual specimens do not establish the germination requirements for a whole species by any means. After completing these studies the author found himself in hearty accord with this opinion.

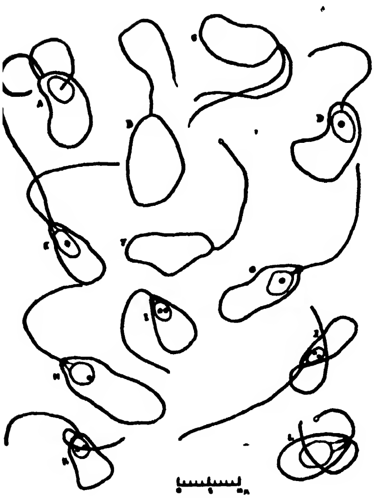
Germination was carried on in hanging drop cultures in Van Tieghem cells or more effectively in culture slides. The latter method was found to the most satisfactory in a number of cases for the reasons that when germination takes a period of several days, condensation on the coverglass, in a hanging drop culture, will allow the drop containing the spores to spread and sometimes be lost by running down the side of the cell. Furthermore, in cases where there seems to be a mass action effect in the germination, the culture slide allows one to use a greater number of spores than is possible or practical in a hanging drop. Temperature was controlled during germination by the use of incubators

and refrigerators when necessary but germination was often carried on at room temperature. Specific methods of obtaining germination for each organism will be discussed farther on in the paper.

Swarm cells to be stained for flagellar structures were collected by means of a micro pipette and placed on a very clean slide. These swarm cells were killed and fixed by inverting the slide over the fumes of a two percent solution of osmic acid. The smear was allowed to dry for several hours and then stained by the Löffler method as modified by Couch (6, 7). The time of mordanting and staining was modified according to trial and error to obtain the best results. In general it was found that mordanting for a maximum time and staining for a minimum time resulted in a sharper staining with less precipitation of the stain on the slide. Having the slides meticulously clean will also help prevent the stain's precipitating. After staining, the preparations were left in a desiccator over night and then mounted in Canadian balsam with a number one cover slip.

Cytological stains were made in cases in which it was necessary to determine whether biflagellate swarm spores were abnormal or were in a stage of division and also to study the neuromotor apparatus. These preparations were stained by an adaptation of the method developed by Cotner (5). The strength of the stain was varied somewhat. It was found that the zoospores of the Mycetozoa stain more readily than most other zoospores and a weaker stain was more satisfactory. Smears were prepared in the same way as when the preparations were to be stained by the Löffler method. Rather than introducing a drop of stain into the drop of water containing the dead zoospores as Cotner recommends, it was found satisfactory to apply the stain to the dried smear. After staining, the slide was placed in a desiccator for twenty-four hours, cleared with clove oil and mounted in Canadian balsam. Slides to demonstrate whiplash flagella were made using the method recommended by Couch (6), although the author had good results with the Löffler stain for demonstrating both whiplash and tinsel flagella.

The slides were studied under high dry and a clearite oil immersion objective and drawings were made with the aid of a camera lucida.



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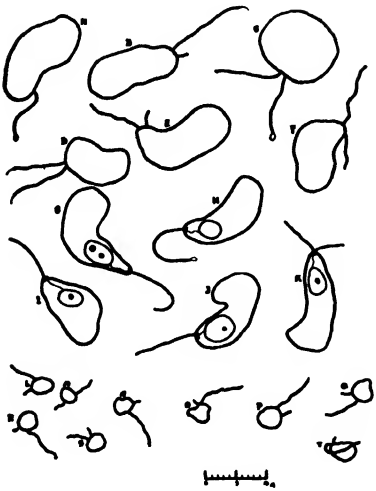

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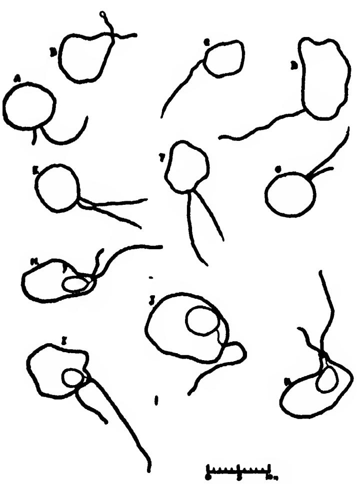

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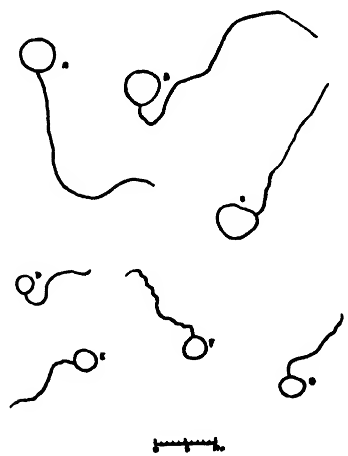

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FIG. 1. *Stemonitis ferruginea.* FIG. 2. *Stemonitis fusca,* and *Plasmodiophora Brassicae.* FIG. 3. *Fulligo septica.* FIG. 4. *Nowakowskiella* sp., and *Synchytrium decipiens.*

OBSERVATIONS

Stemonitis ferruginea Ehrenb. The specimen of *Stemonitis ferruginea* used was obtained from Mr. John M. Roberts and was collected by him in Indiana in July 1940. It was stored for approximately two years with no particular attempt to keep the spores viable. When germination of the spores was attempted in January 1942, they were found to germinate readily in distilled water at room temperature. This germination was carried on in hanging drop cultures using garden hose washers in place of the glass Van Tieghem cells. The first germination was observed after forty-eight hours and the spores had germinated up to eighty per cent in fifty-four hours. It is interesting to mention that all attempts to germinate spores from this specimen, after a year's time from the original attempt, failed. Zoospores were collected in a micro pipette and transferred to slides cleaned in hot, soapy, water and stored in ninety-five per cent alcohol. The importance of having the slides perfectly clean cannot be over-emphasized because foreign material will cause the stain to precipitate on the slide. The zoospores were killed by exposure to fumes of two per cent osmic acid for thirty seconds. The slides were allowed to dry in an inverted position. This has the advantage of allowing the zoospores to become better distributed over the slide because it helps prevent them from being attracted to the periphery of the drop. A number of smears were taken for staining. The time of mordanting and staining was varied. Slides selected as being most satisfactory had been treated with the mordanting solution for three quarters of a minute and stained for one and one half minutes. Cytological stains were made by treating a dried smear for five minutes with a five tenth per cent aqueous solution of crystal violet. The stain was washed off with distilled water and the slide allowed to dry for forty-eight hours in a desiccator. The slides were then cleared with clove oil and mounted in Canadian balsam.

Three types or modifications of the flagella were discernable on the slides stained with the Löffler stain. They were as follows: approximately 56 per cent were of the ordinary blunt-ended type; 44 per cent had the knobbed type of flagellum. Biflagellate zoo-

spores occurred in the ratio of fifteen biflagellate to seven hundred and sixty uniflagellate or 1.9 per cent. Of these biflagellate zoospores the flagellate were of various types as follows: both flagella stubbed; one stubbed and one whiplash; one stubbed and one knobbed. Combinations that were not found were those having two whiplash flagella or a whiplash plus a knobbed flagellum. No tinsel type of flagella were found.

The cytological stain showed a large, dark-staining nucleus present in all cells. It was invariably located in the anterior or flagellar portion of the cell. A darker staining endosome is usually present and in some cases two are present. The number of endosomes in the nucleus seemed to have no correlation with the number of flagella. In no case was there more than one nucleus present. Neither was there any indication that the nucleus was preparing to divide or was in any stage of division.

There was no apparent difference in the neuromotor apparatus of the uniflagellate and biflagellate cells. Even in the uniflagellate zoospores the neuromotor apparatus was clearly of a potentially dual nature. This supports the investigations of the Japanese mycologists Sinoto and Yuasa who contend that the zoospores of the Mycetozoa, whether uniflagellate or biflagellate, have two blepharoplasts (**17**, **23**). Two blepharoplasts are present each with a rhizoplast connecting it to the nucleus. Each blepharoplast gave rise to a flagellum in the biflagellate zoospores. There was no apparent difference in the blepharoplasts whether they produced a flagellum or not.

The zoospores were in various stages of becoming amoeboid. Practically all of the zoospores showed the formation of pseudopodia while still in the actively swimming or flagellated state. Other zoospores were seen that had completely lost their flagella and were carrying on locomotion exclusively by pseudopodia. In these cases the entire neuromotor apparatus had disappeared.

Stemonitis fusca (Roth) Rost.: The specimens of *S. fusca* used in the flagellar studies were collected on the Michigan State College Campus in East Lansing. They were collected in April and germination studies were carried on immediately after collection, in hanging drop cultures. It was found that the spores germinated readily in either sterile river water or distilled water at

twenty-eight degrees centigrade. Temperatures either lower or higher did not give as good results. Approximately seventy per cent of the spores germinated under these conditions within ninety-six hours. Little or no germination was obtained at room temperature.

Flagellar and cytological stains were made as for *S. ferruginea*. The relative time of mordanting and staining which gave most satisfactory slides was found to be the same as for *S. ferruginea*.

On those slides stained by the Löffler stain three modifications of the flagella were observed. They were as follows: approximately 30.4 per cent were of the plain type; 14.8 per cent were of the whiplash variety, and 46 per cent were of the knobbed variety. Biflagellate zoospores occurred as about 8 per cent of the total. In the biflagellate zoospores the flagella occurred in the following combinations: plain plus plain; plain plus whiplash; plain plus knobbed; whiplash plus knobbed; whiplash plus whiplash. None were seen in which both flagella were of the knobbed variety. In no case was a flagellum present of the tinsel type. The relative length of the flagellum seemed to have no correlation with the type.

Zoospores of *S. fusca* were the best studied as far as the knobbed flagellum was concerned. These zoospores exhibited the condition in a greater number of cases than zoospores of any other genus or species. It is difficult to say what this modification represents. Knobbed flagella have been observed on members of the Chytridiales and interpreted variously as abnormal forms due to degeneration and old age or due to immaturity (1, 8, 12). None of these explanations can be regarded as applicable in this case. The percentage of zoospores having the knobbed flagellum was seen to be as great in young, newly germinated cultures as in old. The percentage remained approximately the same in cultures germinated in both distilled water and in river water. The temperature during germination did not affect the percentage. Spores from other specimens were used to make sure that the condition was not due to a peculiarity of an individual specimen. The knobs on the flagella were observed by Dr. Bessey and myself on living zoospores thus removing the possibility that the feature was due to the treatment the zoospores received during the killing and staining processes.

Without additional investigation it would be difficult to make an authoritative explanation of this type of flagellum. Many authors regard the flagellum and the pseudopodium as homologous. If this is true then the sheath of the flagellum would represent the ectoplasm of the pseudopodium and the central cylinder the more fluid endoplasm. If the cylinder, or endoplasm, were for some reason more fluid than is usually the case, a slight extension, instead of remaining as a whiplash, would tend to collect into a drop or knob at the end of the flagellum due to surface tension. This idea is supported in part by the fact that those species having the knobbed flagellum on some of their zoospores have whiplashes on other zoospores. Thus the knobbed flagellum, as seen during these studies, may represent a modification of the whiplash type and not a third and distinct type of flagellum. It must not be regarded in all cases as being an abnormality due to age, environment, etc. It would be interesting to investigate this problem further and determine whether the knobbed condition of the flagellum is characteristic of any particular groups, particularly the Mycetozoa.

In *S. fusca* the dual nature of the neuromotor apparatus is not as evident as it is in *S. ferruginea.* All zoospores remain potentially biflagellate in that they have the usual two blepharoplasts. However, only one of the blepharoplasts has a rhizoplast connecting it to the nucleus. Exactly the same condition is found in the uniflagellate zoospores except that in the former case both blepharoplasts of course produce a flagellum.

A large nucleus is invariably located in the anterior portion of the cell. This nucleus has a darker staining endosome present and occasionally two. There is no apparent correlation between the number of endosomes in the nucleus and the number of flagella on the zoospore. In no case was there anything to indicate that the biflagellate zoospores were in a state of division.

Pseudopodia were present on most zoospores and the zoospores were seen in all stages of becoming amoeboid. In those in which the flagella had been completely absorbed the neuromotor apparatus had likewise degenerated.

Fuligo septica (Linn.) Gmel.: Specimens used in the study were collected shortly after the formation of the sporangium. These

germinated in 96 hours in both distilled water and in sterile river water at room temperature and also at 28 degrees centigrade. The time of germination was cut down to 48 hours at room temperature by wetting and drying the spores. This was the only one of the many slime molds worked with which was induced to germinate in less time by the wetting and drying method as recommended by Jahn (**13**).

Three modifications of the flagellar structure were found in the following proportions: 52 per cent of the whiplash type; 47 per cent of the blunt ended type; and less than one per cent of the knobbed type. Since these are probably all modifications of the whiplash type it might be more accurate to say that all were of the whiplash type. None of the zoospores had flagella of the tinsel type.

Biflagellate zoospores were common, amounting to about 26 per cent of the total. These had the following combinations of flagella: blunt ended plus blunt ended; blunt ended plus whiplash; whiplash plus whiplash; and blunt ended plus a knobbed flagellum. A combination not observed was whiplash plus knobbed. The relative length of the flagella varied from markedly heterokont to isokont.

Like the other members of the Mycetozoa studied, two blepharoplasts were always present in both the uniflagellate and the biflagellate zoospores. In the case of the biflagellate condition each of the blepharoplasts produced a flagellum. Only one of the blepharoplasts had a rhizoplast connecting it to the nucleus, however, in the case of the uniflagellate as well as the biflagellate zoospores. In this regard the zoospores resemble those of *Stemonitis fusca*. In the uniflagellate zoospores the single rhizoplast connects the nucleus and the blepharoplast which produces the flagellum. A rather large but lightly staining nucleus is present in the anterior part of the cell. No endosomes were observed in the nuclei. There was no indication that any of the biflagellate zoospores were in a stage of division. None of the zoospores had flagella of the tinsel type.

Plasmodiophora Brassicae Woronin 1848: The flagellar structure of *Plasmodiophora Brassicae* is of particular interest at the present time due to a tendency on the part of some authors (**14**)

to place the genus in the family Woroninaceae. This is done largely on the basis of Ledingham's research (**15**, **16**) which showed that some genera of the Plasmodiophorales (*Plasmodiophora* and *Spongospora*) had two flagella rather than one as in the original description. It has been shown, however, that the slime molds as a group are potentially biflagellate in that they have two blepharoplasts and often possess two flagella (**9**, **17**, **23**). Consequently the possession of two flagella should not necessarily make it impossible to consider the Plasmodiophorales as being allied to the slime molds. As some other members of the Woroninaceae have been shown to have a tinsel type of flagellum and the slime molds have only the whiplash or modified whiplash type, the presence or absence of the tinsel flagellum on *Plasmodiophora* should be a diagnostic character of some importance and would tend to confirm its inclusion in the Woroninaceae group on the one hand or its alliance to the Mycetozoa group on the other.

Zoospores used in this study were obtained by germinating spores from infected roots. A number of different methods recommended in the literature for obtaining germination of the spores were tried with little success. Chupp (**4**) recommended germinating the spores in a muck soil filtrate (pH not specified) and incubating them at an optimum temperature of 28 degrees centigrade. He found that germination dropped rapidly as the incubation temperature was lowered and he was able to get little or no germination at room temperature. He was unable to obtain infection of cabbage seedlings in the greenhouse during the winter. He was also unable to obtain germination of the spores in distilled water. Wellman (**27**) on the other hand found the optimum temperature for germination to be not over 25 degrees centigrade with the percentage of germination dropping off rapidly as the incubation temperature was raised. He recommended that the spores be germinated in considerable quantity because there seemed to be some mass effect. He reported germination as being good in distilled water. Ledingham, in a letter to the author, reported that he found germination to be satisfactory when the spores were wet and dried a number of times and then incubated at room temperature in tapwater with a pH of 8. He used distilled water also and obtained satisfactory germination. He recommended that

the spores be germinated in considerable quantity because of the mass effect. These ways were tried as recommended and many others including the placing of sterile, excised, root tips in the cultures in hope that the presence of the living host tissue might have a stimulatory effect on the spores. Rain water and melted snow water were tried. The pH was manipulated by adding small amounts of lactic, acetic, and hydrochloric acid to the various media. Minute amounts of hydrogen peroxide were added to the media in an attempt to supply oxygen to the spores. Oxygen and air were bubbled through the cultures in an attempt to induce germination. Results were either entirely negative or the germination was so very slight that it was impossible to obtain the zoospores. A spore was once observed germinating, by Dr. Bessey and myself, which had become attached to one of the root hairs of an excised root placed in the culture. The spore case was seen to be split and a small amount of protoplasm had oozed out. Attached to this bit of protoplasm two actively beating flagella could be detected. Unfortunately this zoospore was lost in attempting to transfer the rootlet from the culture dish to a slide for staining. Our observations confirm those of Wellman (**21**) on the germination of the spore. He reports that flagella are produced almost immediately after the first bit of cytoplasm comes through the break in the spore case and from that time on the partially germinated spore swims about actively. As considerable time may elapse before germination is completed it makes the last stages of this process exceedingly hard to observe. It is not altogether surprising that spores of *P. Brassicae* should vary in their requirements for germination because of the existence of physiological races in this organism.

The best germination obtained was obtained under the following conditions: infected roots which had been frozen and thawed several times over a two month period were macerated in a mortar. Distilled water was added and the mixture stirred up to place the liberated spores in suspension. The coarser material was allowed to settle to the bottom and the supernatant liquid with the spores in suspension was decanted off and strained through cheese cloth. It was then placed in the centrifuge and rotated slowly to throw the coarser plant material to the bottom. The

spore suspension was then poured into another centrifuge tube and centrifuged again, this time more rapidly so that the spores were thrown down. The water containing most of the bacteria was then poured off. Sterile distilled water was added and the spores stirred up into a suspension again. They were centrifuged once again. This washing was repeated a number of times depending on how numerous the bacteria were originally. The spores were eventually left to germinate in a Syracuse watch glass containing sterile distilled water made just acid by adding acetic acid with litmus paper as the indicator. The spores were incubated at twenty-five degrees centrigrade. On the third day a fair degree of germination had taken place.

Zoospores to be studied for flagellar structure were collected, killed, and stained with the Löffler stain and Couch's whiplash stain in the same way used for the slime molds. Those slides selected as most satisfactory of those stained with the Löffler stain were those that were mordanted for forty-five seconds and stained for one minute.

The zoospores were all of the biflagellate type and in most cases markedly heterokont. In some of them the shorter flagellum was so reduced as to be almost unnoticeable. In one zoospore found, the two flagella were very nearly isokont. The flagella were in all cases of the blunt ended type. No tinsels or whiplashes were to be found on any of the flagella.

Nowakowskiella sp. The zoospores were obtained from a culture that had been maintained in the laboratory for about a year. Those zoospores to be studied for flagellar structures were handled and stained with the Löffler stain in the same manner as described for other zoospores. The best results were obtained by treating the slides with mordant for three quarters of a minute and with the stain for half a minute.

Two types of flagella were observed on the slides stained by the Löffler stain and also on the slides stained by the Couch whiplash stain. These were the definite whiplash type and the blunt ended flagellum. The whiplash varied in length from very short to some having the whiplash as long as the flagellum proper. It was found that in the cases where the whiplash was extremely long there was a corresponding reduction in the length of the flagellum proper.

Less than one per cent of the zoospores had two flagella. These flagella were either of the whiplash or blunt ended in all combinations. No tinsel flagella were found. These abnormally biflagellate zoospores were uninucleate and therefore are not comparable to the binucleate zoospores described by Cotner for *Blastocladia* which were due to the failure to complete the cleavage into the normal, uniflagellate, uninucleate cells. What is the cause of this abnormal doubling of the flagella has not been determined.

Synchytrium decipiens Farlow: The specimen used was collected by Dr. Bessey on a leaf of *Amphiocarpa dioica*. The zoosporangia were scraped from the sori on the leaf and transferred to a drop of distilled water in a hanging drop culture where they germinated in three hours at room temperature. The zoospores were collected, killed, and stained by the Löffler stain and Couch's whiplash stain in the same manner as mentioned before.

Only uniflagellate zoospores were found to occur. The flagella of these were all of the whiplash or blunt ended type. The whips were relatively short, varying from none at all to about two microns in length. Approximately fifteen per cent had no whiplash at all.

SUMMARY AND CONCLUSIONS

Mycetozoa and *Plasmodiophora:* The work done on this problem has confirmed the contention of Sinoto and Yuasa (**17, 23**) that the swarm cells of the Mycetozoa have two blepharoplasts. It shows that the Mycetozoa may be regarded as potentially biflagellate and that as Gilbert (**9**) and the Japanese authors, mentioned above, pointed out, two flagella are frequently found on the swarm cells. The writer definitely demonstrated their presence in *Stemonitis ferruginea, S. fusca* and *Fuligo septica.* It establishes the type of flagellum for these forms and by inference the entire Mycetozoa as being the whiplash type or a modification of that type, *i.e.* blunt ended or knobbed.

A germinating sport of *Plasmodiophora Brassicae* was seen to have two actively beating flagella, thus confirming Ledingham's investigation that indicated that the zoospores of *P. Brassicae* were biflagellate. The investigations of the flagellar types of this swarm cell lend support to the view that their flagellation is of the My-

cetozoa type. Certain authors wish to place the members of the Plasmodiophorales in the family Woroninaceae. Some members of this family, however, have been shown to have the tinsel type for one flagellum and the whiplash type for the other. In view of this, *P. Brassicae,* the type genus and species of the Family Plasmodiophoraceae and the order Plasmodiophorales, must be excluded from relationship to the Woroninaceae due to its type of flagellation.

Synchytrium decipiens and *Nowakowskiella* sp.: This investigation shows the flagellar type of these two genera to be of the whiplash type. This lends support to the assumption that the flagellar type for the Chytridiales (in the narrow sense of the term) is of the whiplash or modified whiplash type.

Certain authors homologize the flagellum and the pseudopodium. It is the author's opinion that on the basis of this hypothesis one is able to homologize the blunt ended, knobbed, and whiplash flagellum. The knobbed flagellum, as described in the literature prior to this paper, is described as an abnormal and degenerate condition due to age etc. This is clearly not the case in the organisms reported in this paper as having the knobbed type of flagellum. The indication is very strong that the knobbed flagellum is a modification of the whiplash type and not always degenerative in its nature.

This research was carried on under the supervision of Dr. Bessey and the author would like to express his thanks and appreciation to Dr. Bessey for suggesting the problem and for the aid and inspiration given during the entire course of the research, also for his help in the preparation of this article.

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FIG. 1. *Stemonitis ferruginea* Ehrenb. A, B, C, and F stained with the Löffler stain, D, G, H, I, J, K, and L stained with a crystal violet cytological stain. B and C show the whiplash type of flagellum. F and L the knobbed flagellum.

FIG. 2. A to K, *Stemonitis fusca* (Roth) Rost. A to F stained with the Löffler stain, G to K with the crystal violet cytological stain. A, G, and H show the knobbed flagellum, B and D the whiplash flagellum. L to T, *Plasmodiophora Brassicae* Woronin. All are stained with the Löffler stain and show the blunt ended type of flagellum.

FIG. 3. *Fuligo septica* (Linn.) Gmel. A to G stained with the Löffler stain, H to K with the crystal violet cytological stain. B shows the knobbed type of flagellum, C, E, F, and G show the whiplash type.

FIG. 4. A, B, and C, *Nowakowskiella* sp. All stained with the Löffler stain. B and C show the whiplash type of flagellum. Note the extreme development of the whiplash in C. D to G, *Synchytrium decipiens* Farlow. All stained with the Löffler stain. E, F, and G show the whiplash type of flagellum.

MYCOLOGY PRESENTS PENICILLIN

CHARLES THOM

A conservative medical official recently told a technical audience that "Penicillin is the most potent agent" * * * "ever encountered, which produces no bad effects upon the patient." He then listed as conspicuous among microbial enemies of man which respond to penicillin, *Gonococcus, Meningococcus, Streptococcus hemolyticus* and *S. viridans, Pneumococcus, Staphylococcus, Clostridium tetanus* and *C. Welchii, Corynebacterium diphtheriae* and *Actinomyces bovis.* Such a list justifies the caption "miracle drug" put upon it by another medical scholar who is rarely swayed by impulse. I am asked to trace the mycological history of the discovery and development of penicillin to its present place among things worth while. Since there are some misunderstandings as to its early history, the data will be presented in as verifiable order as possible.

The first ten years. In 1929, Alexander Fleming reported the discovery and naming of penicillin. The essential facts of this discovery consisted (1) in the observation that a particular mold growing as a contaminant in a culture of *Staphylococcus aureus* inhibited the bacterium, *i.e.* that the *Staphylococcus* could not grow in a zone surrounding the mold colony. This observation was already well known as a phenomenon seen frequently when molds and bacteria are found growing together. Most commonly the observation is reversed—a mold fails to develop normally, if at all, in the presence of large numbers of bacteria. (2) Fleming went further and showed that the mold had produced an inhibiting substance in the nutrient substratum which could be separated from the fungus itself and used to inhibit certain bacteria. He tabulated a series of bacteria susceptible and other bacteria resistant to the inhibiting substance. (3) Since the mold was a species of the great genus *Penicillium,* he called his inhibiting substance penicillin. (4) Not being a mycologist, he undertook to

identify his mold from the literature and selected the name *Penicillium rubrum* Biourge which was published for it in his 1929 paper. (5) He described the use of penicillin in laboratory practice as facilitating the culture of certain gram-negative organisms by inhibiting their most usual gram-positive accompanying species.

Fleming did not pursue the chemical study of penicillin, survey its production by other molds, or by other strains of the same species. In subsequent papers (1931, 1932, 1936) he elaborated his studies upon the same general line with the same strains but did not broaden the field greatly.

The Fleming organism comes to America. On April 29, 1930, Prof. Harold Raistrick of the School of Tropical Medicine in London wrote as follows to Thom in Washington: "The other culture, labelled *P. rubrum* (?), was received from the British National Collection of Type Cultures and bears their catalogue number *3127*. It was originally isolated by Dr. Alexander Fleming of St. Mary's Hospital, London, and is described by Fleming in a paper * * * (see citation). I am carrying out a piece of work on this species and since, as you will see if you refer to the original paper, this diagnosis of it is very doubtful, I wonder if you would be good enough in this case to let me have an authoritative statement as to its identity." A culture of the Fleming organism accompanied the letter. From this letter it is clear that Fleming's culture was in the hands of St. John Brooks before April 1930. Raistrick's laboratory began work with it before May 1, 1930, hence it was available to any worker. Raistrick, from his own knowledge of molds, did not accept the identification of this organism as *P. rubrum* (either according to Stoll or to Biourge). To that letter, I replied (June 30, 1930): "For this other culture, however, I am obliged to you since I was anxious to know what Fleming's organism would be like. I have cultivated it under several different conditions and cannot agree with his nomenclature as *P. rubrum* either in the sense of my 1910 paper or in the sense of Biourge's Monograph. In fact, I believe his culture, although showing some divergences in culture reaction, to be closer to *P. notatum* of p. 264 in my book than to the group discussed on pages 249 to 250 as indicated by the nomenclature used" (by Fleming). The culture received from Raistrick was put in

the Thom collection as *144.5112.1*. The corrected name appears in Raistrick's papers and was accepted by Fleming in his 1932 paper. Nevertheless, requests for *P. rubrum* were frequently received during the several succeeding years. These were usually answered by sending the Fleming culture and a letter explaining the corrected nomenclature.

The importance of corrected nomenclature here lies in the fact that recognition of Fleming's organism as one of the great and universally distributed *Penicillium chrysogenum-notatum* group opened at once, as we saw it, the possibility that research among related organisms would show penicillin production to be common to the group, hence would enable us to choose among available penicillin-producing forms. Raistrick was at that time the outstanding advocate of the specificity theory in biochemical reactions. His hypothesis was that the formation of a particular biochemical product was tantamount to proof that a particular species of mold was present as the producing agent. The product was assumed to be unique to the species; conversely, absence of the special product was proof that the mold did not belong to the species. Hence a chemical analysis could be depended upon to disclose the identity of the mold responsible for the findings. In his dealings with us his analysis had actually caught mistaken identifications often enough to give it presumptive value. Rigorous comparative work with cultures seems to prove that strains morphologically identifiable as members of a related series may be expected to produce reactions of the same kind or nature, but that these individual reactions may differ greatly in quantitative expression. Concretely it has been shown that among penicillin producers, the amount produced by one strain may be 100 times as great as that produced by another, or, under a standardized routine, one may produce abundantly, another give no penicillin. But there is fair reason to believe that under adequate investigation all related forms will produce the substance unless the capacity has been entirely dropped by mutation. The *P. notatum* series *does* mutate conspicuously. Specificity definitely fails when we find what seems to be real penicillin produced by strains of *Aspergillus flavus* and *A. flavipes* representing not only another genus but two quite contrasting groups within that genus. In the case

of penicillin, the English workers long insisted that penicillin is produced only by Fleming's organism and its derivative strains. Finally, however, Raper, Alexander, and Coghill, working in Peoria piled up proofs that strains isolated from soil and other substances from widely separate regions would produce it, and finally that some of them would produce it in considerably greater quantity. Strangely enough the Fleming strain and its derivative or substrains remained the best producers of penicillin for many months after the collection and testing of other members of the *chrysogenum-notatum* group began. In spite of fantastic stories of its single appearance in St. Mary's Hospital Laboratory, one familiar with the inhibition of mold cultures by bacteria is compelled to believe that *P. notatum* was an "old settler" there, which survived by mutation and selection until at last one member of the lot was conspicuously able to "hold its own" against its bacterial competitors.

So much for one strain, the Fleming organism, and its emigration to America. It was distributed from the laboratory in Washington by Thom and Raper to all who asked for it from 1930 onward. How many other transfers from the English type culture collection reached America we do not know but none have come to our attention. There is one reference to Bornstein as obtaining his culture from Fleming. In a file of letters before me, we have the record of its distribution to great university laboratories, hospitals, and to manufacturing chemists who are now producing penicillin.

The next strain that we know about (also a Fleming derivative) was brought to America by Drs. Florey and Heatley and delivered to me personally on July 9, 1941. To ensure a separate record it entered the collection as *144.5767*. It was passed by Heatley to the Northern Regional Laboratory at Peoria and to an unlisted number of manufacturing laboratories, hence derivatives from Heatley's strain may appear anywhere.

This digression from the story is made merely to record the story of the penicillin-producing culture. We return now to the development of our information about penicillin.

As indicated in Raistrick's letter already quoted, his laboratory began to study penicillin in 1930; this work was reported by Clut-

terbuck, Lovell and Raistrick in 1932. They included *P. chrysogenum* Thom and *P. notatum* Westling (type) strains, with Fleming's strain and grew the three molds under their standradized procedure. No penicillin was obtained in their cultures of *P. chrysogenum* and *P. notatum* (Westling's strain); they therefore concluded that penicillin is a product unique to Fleming's organism. They identified and discussed chrysogenin as the yellow pigment produced by *P. chrysogenum*. This pigment is produced so commonly along with penicillin that its presence is often regarded as indicative of a profitable culture. It is also produced without penicillin, hence the correlation is not entirely dependable. While Raistrick's group believed their culture methods and their chemical work had paved the way to the analysis of penicillin, they did not complete the study. The instability of penicillin, together with the very small yield per unit of material used, appears to have led them to close their investigation.

Roger D. Reid obtained his first culture of the Fleming organism from us in November 1930, another transfer in July 1931. His studies published in 1933, 1934, and 1935, covered the conclusion that penicillin is bacteriostatic instead of bacteriolytic, and detailed its reactions to light, gases and temperature, effects of distillation, dialysis; in the main they confirmed and extended the work of Fleming, and of the Raistrick group without going beyond the chemical and bacteriological laboratory aspects and without suggesting possibilities of development to major usefulness. There is a gap in publication concerning penicillin between Fleming's note to the Second International Congress of Microbiology in 1936, and 1940. Survey of laboratory correspondence during the period from 1933 to 1940 shows that requests for Fleming's organism came from a number of the great laboratories engaged in bacteriological research but not from the pharmaceutical manufacturers. Their immediate response to Florey's paper in 1940 suggests that they had not previously obtained the organism from other sources. In this period then whatever work was done in the laboratories using *Penicillium notatum* was not reported except the paper of Bornstein who tested penicillin against "Enterococci and other Streptococci."

Florey in his recent paper (Endeavor 111 (9): 3–14. Jan. 1944) records that his group began to work on penicillin in 1938. This study was reported in the *Lancet* Aug. 24, 1940 by Chain, Florey, Gardner, Jennings, Orr-Ewing, Sanders, and Heatley. Thus Florey seems to have inspired the work done by a considerable group of workers in Oxford University and in collaborating hospitals. For the purpose of the moment, we will disregard the mass of constructive biochemical and bacteriological work done by the group. The pharmacological work detailed in that paper, followed by the 1941 report by Abraham, Chain, Fletcher, Gardner, Heatley, Jennings, and Florey, aroused widespread interest. Turning again to the laboratory file, requests for Fleming's organism for use by manufacturing chemists began in a letter dated Sept. 23, 1940, another Oct. 1, 1940. One university laboratory asked for it August 21! Was there any connection? Within a half year after the publication of the 1941 paper, laboratories and pharmaceutical houses well distributed in the United States and extending to Mexico and Brazil were supplied with transfers of the Fleming organism (*144.5112.1*).

One phase of the work of the Oxford group must be briefly presented. To facilitate comparison of the results of successive cultures and the value of solutions of unknown origin an assay method was devised by Dr. N. G. Heatley.—As described in outline of Florey:

"An agar plate is seeded with the test organism—*Staphylococcus aureus* has been used as a routine—by pouring on a broth culture of the organism, draining off the excess, and drying the plate for 1–2 hours in the 37° C. incubator with the lid raised. Short open-ended cylinders of glass or vitreous porcelain are then placed on the surface of the agar, and the solutions to be assayed are placed in the cylinders. After incubation, the surface of the agar becomes covered with a continuous film of bacterial growth except for a circular zone around each cylinder where the penicillin has diffused out and inhibited growth. The diameter of this zone is related to the concentration of penicillin in the solution in the cylinder, and by setting up solutions containing known amounts of penicillin a curve relating the two can be drawn. The actual diameter of the zone produced by any given solution varies slightly from day to

day, since it depends on a number of factors, some of which are difficult to control in practice; but the variation can be countered by including one or more solutions of known strength in each assay.

"For the same reasons which apply in the case of other biologically active agents of unknown purity, it was found convenient to express the antibacterial activity of penicillin in terms of some standard preparation of penicillin. The 'unit' originally taken for convenience in this laboratory, only, has since been adopted as the 'Oxford unit' by some other workers. It was defined originally as that amount of penicillin contained in 1 ml. of a certain purely arbitrary stock solution. The latter was exhausted long ago, but other primary standards, in the form of dry preparations, were standardized against it. Until penicillin is obtained in a clearly characterizable form the only way in which the potency of a given solid or liquid preparation can be measured in terms of Oxford units is by a direct comparative assay against a preparation containing a known number of these units."

Penicillin—comes to America. While the 1941 paper was still in press, Dr. Florey obtained the support of the Rockefeller Foundation in London (see *R. F. Review* for 1943) and was sent with his associate, Dr. N. G. Heatley, to New York in July 1941. There are discrepancies in the stories told as to what happened in New York. We know from our laboratory records that certain manufacturers already had Fleming's organism and may infer that they were already working with it. Enough that Florey and Heatley did not establish American connections from the Rockefeller offices in New York. The Rockefeller Foundation sent them to the Medical Section of the National Research Council in Washington on July 8, 1941. Since problems concerning *Penicillium* had long been handled in the Department of Agriculture, the project was referred to us directly by telephone. Arrangements were completed by telegraph on July 9th to turn the project over to the Northern Regional Research Laboratory of the U. S. Dept. of Agriculture at Peoria, Illinois, and on July 13th Florey and Heatley were in the Peoria Laboratory where they had the coöperation of a group of men with long experience in mold fermentation, including Herrick, May, Coghill, Ward, Raper, Moyer, and others.

Florey stayed only a few days, then turned to other interests; Heatley continued in Peoria for a time, then visited a number of large manufacturers in the effort to stimulate production. He worked in one plant for several months before returning to England.

Thus the penicillin project reached America and fell into the hands of a great government laboratory from which has come most of the fundamental work that has made large scale production possible.

The problem of production became a study in mold physiology in which our measure of success has directly represented the accuracy of our delimitation of these problems and the adjustment of our procedures to the fundamental principles determined. Some of the problems encountered in developing penicillin must be discussed.

Aerobiosis. Penicillium notatum is aerobic. It grows in nature upon the surface of a substratum—floats as a scum or blanket of mycelium upon fluid or forms a velvety green mat on solid or semisolid food. Its hyphae penetrate normally perhaps one or two millimeters but are restricted from going more deeply by lack of air. Naturally, then, the first development of penicillin production was "still" culture—colonies grown in broad bottomed flasks, shallow pans, milk bottles, etc. Effective use of the food material was found in layers less than 25 mm. (1 inch) deep. To handle a large volume of culture substratum in such shallow culture, enormous areas must be grown. This required thousands of bottles or flasks; hence represented a cumbersome process expensive in labor, but produced a favorable yield. Such producing plants were quickly established and yielded most of the penicillin produced in America from 1941 to the end of 1943.

Ventilation. The excess of carbon dioxide produced necessitates the maintenance of a constant flow of air free from other molds and bacteria. The necessary sources of pure air, filters and circulating machinery are usually closely guarded secrets of factory installation.

Pure culture. Penicillium notatum is a vigorous grower only under optimum conditions. At best many other molds if present will overgrow it and destroy the product. Penicillin inhibits

gram-positive bacteria but not the commonest gram-negative species. The ubiquitous *Escherichia coli* if it enters as a contaminant will render a culture worthless. Rigorous exclusion of other organisms is essential in handling penicillin production.

Variability. Most strains of *Penicillium notatum* are exceedingly unstable. In miscellaneous culture variants or mutants are very common. To maintain continuous production, standardized culture must be developed to maintain a dependable strain. Without such care, the stock may deteriorate and become worthless for penicillin production.

Selected strains. Systematic selection of variants from the Fleming organism resulted in greatly increasing the yield above that obtained by the Oxford workers but the limit was soon reached and the yield per litre of solution was still fantastically small. Surveys have therefore covered thousands of samples of soil from widely separated regions and moldy substances wherever found. Fleming's organism has been replaced already by better yielding strains and thousands of new strains have been tested in Peoria, Madison, Minneapolis, Cold Spring Harbor, Palo Alto, and elsewhere. Radiation of cultures by many procedures is being tested. No one knows where the limit may fall. In the main the results of radiation merely increase the number of variants handled without greatly increasing the yield beyond that produced by strains met in the survey of natural mold sources.

The culture medium. *Penicillium notatum* is widely distributed in nature. It appears in culture from soil, especially in rich cultivated soil since it depends on organic remains for growth. It is fairly common in or on miscellaneous food stuffs. In pure culture it will grow upon many types of culture media and usually produce some penicillin. As Florey and Heatley brought their strain to America and grew it on routine media the yield of penicillin was very small. In the hands of the Peoria laboratory it was quickly shown that the addition of a small percentage of the "corn steeping liquor" long used in the yeast industry would multiply the yield many times. Sterilized yeast, brown sugar, wheat bran and cabbage juice have been reported favorable. Thus far "corn steeping liquor" ("corn steep") is preferred by all but the few

manufacturers who have had experience with the bran process and claim good results.

Since the exact component of either of these products responsible for penicillin formation is not known, two hypotheses have been offered to account for the findings (a) that penicillin is an extra-cellular product due to agents secreted by the mold acting upon the substratum. Hence penicillin, whether produced by *Penicillium notatum, Aspergillus flavus* or *A. flavipes,* is the result of secreted agents, probably enzymes, acting upon specific materials present in the substratum or (b) the alternative hypothesis which assumes intra-cellular biochemical activities which result in the secretion of penicillin and postulates that the same intra-cellular activities must be present in any mold producing penicillin. Proofs are not at present available.

Temperature. The optimum temperature for penicillin production has been found to be 24° C. Lower temperatures unduly slow the activity; higher temperatures set free destructive agents. In rooms with thousands of fermenting units control apparatus must be adequate to absorb excess heat of metabolism.

Penicillin production marks a physiological stage of the colony. Penicillin appears to be produced at nearly the same stage in mold development as a crop of spores (conidia). Grown as a single colony in the center of a petri dish, *P. notatum* forms a circular colony often showing radiating wrinkles like spokes of a wheel. Biourge called the series Radiata because of this appearance. By the time the colony is three or four days old a definite central area green from ripening spores is evident. During a growing period of ten days or more, the colony shows an outer colorless band or zone, passing over to green very quickly. Hence at 10 days old there will be an overripe central area, a zone of active fruiting and a narrow outer zone of colorless hyphae actively growing away from the green center. Sampled by removing disks with the cork borer, the zone of production is found to coincide in general with the zone of fresh sporulation. Penicillin in these old cultures diffuses out into the culture medium and is detected in the assay plate, for two or three centimeters beyond the margin of the colony. The petri dish colony described shows areas old and even disintegrating, areas of maximum penicillin production, and areas of

mycelial growth not yet at the producing stage. Such a unit is inefficient when maximum yield is the aim of culture.

To make a shallow pan or bottle culture become an effective producing unit, therefore, it is desirable to inoculate with spores spread evenly over the surface and spaced closely enough to insure that the mycelia developing will quickly come into contact, intertwine, and to some degree anastomose to form a complete blanket of mycelium over the entire surface simultaneously. In this way the entire mycelium acting as a unit will reach the physiological stage for penicillin production at one time and present the largest possible opportunity for simultaneous effect upon the medium.

In sugar containing media, *P. notatum* produces acidity—glucose is changed to gluconic acid. If the pH is allowed to fall to 4 or 4.5, glucose-oxidase variously called "penatin," penicillin-B, notatin, etc., is produced. This is much more intensely antibiotic than penicillin but it is also toxic. Cultures kept above pH 6 do not show this toxic substance. Properly buffered to maintain the cultures in the developmental period above pH 6, the pH rises with the maturity of the colony to pH 7, 7.5, 8.0, even to 8.5. Penicillin seems to be mainly produced between pH 7.5 and 8.0 to continue development perhaps to pH 8.3. As the culture reaches pH above 8.3 destructive agencies appear and the penicillin breaks down quickly. Much work upon the activity of the penicillinases concerned in the destruction of this product leaves many points unsettled. In practice, the absolute maximum yield is usually sacrificed to allow a margin for safety.

Submerged culture. Molds of this group germinating below the surface of liquid media commonly form abnormal stringy masses of hyphae without fruit. Nevertheless the advantages of tank culture from an industrial viewpoint lead workers to explore the possibility of conducting mold fermentation under submerged condition. Thus *A. flavus* has long been used in this way. Later Herrick, May, Ward, *et al.*, developed the production of gluconic acid in tanks by *Penicillium chrysogenum*. The way was thus prepared to develop a practice for handling the nearly related *P. notatum* in submerged culture.

Mold physiology is fundamentally the same no matter what we want the organism to do. Our task is to adjust our practice to the demands of the mold. First among these demands is air. On a laboratory scale, a flask 1/4 to 2/5 full of liquid inoculated with a mold may be aerated by placing it upon a shaking machine, or by diffusing air throughout by any standard practice or by a rapid agitation by some stirring machine. Thorough aeration by either method keeps the liquid in rapid motion. The mold spore or mycelial fragment under these conditions becomes a growth center from which cells as hyphal components radiate in all directions. In response to tension, instead of forming long slender thread-like hyphae the cells shorten, increase in diameter so that the mycelial development is not a mat, a membrane or a stringy mass but approximately a globose mass or pellet. The same picture is produced in the shaken tube or flask, or the blown vat containing thousands of gallons of liquid. If the agitation is stopped for a few moments the mass of pellets often occupies 2/3 or more of the volume.

The difficulties of tank production include the necessity of a constant supply of sterile air carried to every drop of the liquid or every pellet of mold, maintenance of the correct temperature against a heightened rate of metabolism, buffering to control the reaction, together with the development of testing methods which will determine the exact physiological condition in the tank of liquid at any time. In other words, the percentage of efficiency of a factory procedure is measured by the perfection of adjustment between that practice and the physiological requirements of the particular strain of mold in use. Readjustments may be expected to be needed every time an untried strain of mold is substituted for one previously successfully handled.

In spite of many losses and delays tank installations were gradually developed and put in operation. By January 1944, production began to be possible on a large scale. Early in the spring of 1944 totals of production per month had reached somewhere in the 100 to 200 billions of Oxford units per month, release of penicillin for civilian use in hospitals followed early in May and marked the end of the developmental period.

In addition to various types of surface and tank culture, the great interest aroused by the publication of Florey's papers and various popular reports led many laboratories to begin work upon the problem, each following lines based upon the background or the imagination of the workers. Some of the proposals had no constructive value—some have made definite contributions. Clifton (*Science* **98** (2533): 21. 1942) in California proposed the use of a type of generator patterned after that used in the vinegar fermentation. In this a trickling stream of culture medium passes slowly through a mass of shavings covered with mold thus constantly replacing the liquid in contact with the mycelium. Clifton did not report work upon an industrial scale. Others have shown that mycelium of *P. notatum* fed by a continuous flow of fresh culture medium can be made to continue producing penicillin for about three times its period of activity shown by surface or "still" culture and a dozen times its effective life in tanks. Whether it is adaptable to an industrial procedure remains unsettled.

Other workers reading Florey's group reports noted that the crude filtrate from cultures of the Fleming organism freed from mold protein and other pyrogens had been used intravenously in England. The raw filtrate had been used directly for external treatment. Both uses were without ill effect. Such materials could be readily prepared in the culture laboratory. While it was recognized that this cruder form of penicillin deteriorated rapidly at room temperatures, it was also known that it could be kept for considerable periods in the refrigerator. It was thus possible for the hospital laboratory to maintain penicillin solutions sufficiently strong to yield good results within the definite limits already known.

Before penicillin in commercial form was released for civilian use, a number of such groups supplied themselves with working materials very effective for routine cases. Work upon this line was not approved by the official coördinator. Refusal to assist the hospital and the civilian in this way was widely condemned as an arbitrary abuse of power, hence was deliberately defied by a number of competent workers who believed that such service could have been rendered without delaying the actual development of

industrial production. With the release of industrially produced penicillin for civilian use, these temporary units will probably disappear.

In another proposal several layers of sterilized gauze were placed in a petri dish, flooded with culture solution, inoculated with *P. notatum*. The hospital group described the procedure and put forward the definite claim that after several days of incubation the whole mat removed from the dish, fastened over the injured area, and kept damp with the culture solution was effective. Although denounced by an official group as dangerous, the grade of workers responsible for this and some other proposals was fully equal to any in the penicillin field. Unfortunately, some popular publications assured people that making penicillin is easy, and requires neither special apparatus nor definite knowledge. Warnings of danger in such cases were amply justified.

Obviously there are two general uses for penicillin: (1) that of external application and (2) introduction into the blood stream. The highly purified industrial product if abundantly available may be used for both purposes but the field of external application offers a series of opportunities and problems not yet adequately covered by public information.

The part played by individuals and corporations in America in the development of penicillin has been deliberately omitted. Where so many individuals and financial interests have been involved and exchange of experimental results has been widely practiced under the pressure of a war program, an attempt to disentangle the contribution of the individual or the corporation toward the results obtained would be futile. It is equally doubtful to a discriminating spectator who has watched the development of practices and listened to the claims, whether any of the "patents applied for" honestly represent valid claims to originality.

Under the pressure of war needs the Office of Scientific Work and Development (OSRD) at Washington brought together those interested in manufacturing penicillin shortly after Florey and Heatley came to America in 1941. Contracts were prepared and signed with all prospective producers of penicillin. Each agreed to the pooling of the results of research and experiment. Coordinators representing the Government visited each laboratory

from time to time and conferences were held for the purpose of hastening production in every possible way. During this developmental period all penicillin produced was declared the property of the United States, to be paid for at specified prices per 100,000 Oxford units. Assignment of penicillin to particular groups covered chemical research, and special study of penicillin for specified groups of diseases. Penicillin was only released for individual civilian cases on appeal to the designated coördinator. The groups concerned in studying the chemistry of penciillin have been kept under contract of secrecy. Within the group, memoranda are marked "restricted." Even the culture media in use are on the list of restricted items. Recovery of penicillin is included in these restrictions. This paper sought to present the mycologist's story of penicillin discovery and development. The chemistry and industrial practices will be left to others.

During the three developmental years twenty-one producing units were approved by the authorities while many applications were not accepted. Something over $20,000,000 were reported to be invested in these industrial plants whose yield today is totalled in hundred billions of Oxford units per month. Most of the workers now concerned in penicillin production were entirely unacquainted with the kind of mold problems now before them, at the start. On the whole this is a remarkable accomplishment when we remember that the most careful surveys during the previous years had emphasized the small yield and instability of penicillin as rendering very doubtful its profitable production by any industrial process.

With penicillin now available through a thousand or more hospitals, it is in reach of emergency cases over the larger part of the United States. Its usefulness has been proved for whole series of diseases. Its limitations are being so carefully defined that its futile use where its failure becomes a calamity will be eliminated.

The successes of the penicillin program have stimulated research in the whole antibacterial field in the hope that supplementary antibiotic substances may be found to reach other needs equally urgent.

PORT JEFFERSON,
NEW YORK

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Note: The literature of penicillin has been covered very fully in the publications of Merck, Squibb, and Winthrop, and in long series of research papers in the Journals of the last three years. No attempt at detailed citation is made here.

THE CUP FUNGUS, CIBORIA CARUNCULOIDES, PATHOGENIC ON MULBERRY FRUITS

H. H. WHETZEL[1] AND FREDERICK A. WOLF

(WITH 4 FIGURES)

INTRODUCTION

A cup fungus, first adequately described as *Sclerotinia carunculoides* (Siegler and Jenkins, 1922, 1923), parasitizes the fruits of white mulberry, *Morus alba* L., throughout the southeastern United States. As is well known, Prof. Whetzel was long a devoted student of disc fungi, especially those that are pathogenic to fruits. Such fungi, according to him, comprise the family Sclerotiniaceae. Furthermore in his unpublished notes the pathogen on mulberry, herein given consideration, is assigned to the genus *Ciboria*, which includes some of the most widely known members of this family.

The junior author's first contact with this organism on mulberry came in 1919 when he encountered it in the Sand Hills region of North Carolina. He next collected it in 1943 from trees grown for shade near Duke University. Here it has recurred abundantly during each of the three consecutive seasons covered by the present studies. This fungus is of such a nature that it undoubtedly will reappear year after year to attack the fruits of these trees.

Because of Prof. Whetzel's wide experience with Sclerotiniaceae, plans were laid in 1943 for a further study of this mulberry fungus. It was contemplated that the results eventually would be published conjointly, but as a consequence of the death of Prof. Whetzel the present report has perforce been prepared by the junior author.

[1] Professor Whetzel succumbed Nov. 30, 1944. His notes dealing with the fungus herein given consideration were made available through the courtesy of Dr. H. M. Fitzpatrick. I am indebted to Dr. Fitzpatrick, in addition, for his suggestions and criticisms in connection with the preparation of this report.

Even though Prof. Whetzel's notes, microscopic preparations, and other pertinent materials have been made available, it is fully realized that the value of this report would have been greatly enhanced had Prof. Whetzel lived to participate actively in its preparation.

HISTORICAL

The first account of this fungus is a statement by an anonymous author which is recorded in The Experiment Station Record (1903). This statement is merely a brief abstract of a paper read by W. A. Orton at a meeting of the American Association for the Advancement of Science. This anonymous abstract states: "W. A. Orton, in a paper read before Section G, described a disease of mulberry fruits which is reported from Georgia, Alabama, and Mississippi. Often as much as 50 per cent of the fruit is affected. The symptoms are peculiarly enlarged portions of the aggregate fruits. The disease is of fungus origin and the point of attack seems to be the seeds which are greatly enlarged. The fungus which is closely allied to *Gloeosporium* was described as a new genus, *Spermatomyces,* the species name *Mori* being given to it."

Apparently this paper by Orton was never published and the fate of the manuscript remains unknown. Curiously no further mention of the disease was made until 1920 when Taubenhaus (1921) published a semi-popular account in which he applied the appropriate descriptive name "popcorn disease." This account contains a brief description of the origin and development of the "sclerotium" and the extrusion of "colorless, roundish spores" in a "stout, gelatinous, whitish grey thread from the tip of each infected drupelet." Later (1937) he employed the name "mulberry swells," a designation that plant pathologists do not seem to consider so satisfactory a name as "popcorn disease." To date the studies by Siegler and Jenkins (1922, 1923) constitute the only ones that have been made from which an understanding of the developmental morphology of this pathogen can be gleaned, and the present purpose is to supplement their findings.

MATERIALS AND METHODS

The mulberry trees used as a source of materials were so located as to be easily accessible to the laboratory; consequently abundant

material was available at all times, an eventuality that greatly facilitated these studies. Progressive developmental changes in the pathogen were therefore followed closely. Some of the material collected for examination was appropriately fixed and was later embedded in paraffin, sectioned, and stained. In most cases Haidenhain's iron alum haematoxylin proved to be the best stain. Erythrosin, when used either alone or as a counterstain, was useful in tinting the gelatinous coating of ascospores and hyphae. However, equally well defined envelopes on ascospores are demonstrable by use of lacto-phenol cotton-blue. As an adjunct in interpreting structural features of sclerotia use was made of freehand sections.

Pure cultures were prepared by isolation from sclerotia, apothecial tissue, and ascospores. Colonies of the pathogen were produced when tissues from sclerotia, that had been surface disinfected, were planted on agar plates. If apothecia are maintained in a humidor in such a way as to provide a high relative humidity, the ascospores are expelled in a "cloud" when the cover is removed. Accordingly advantage was taken of the liberation of ascospores *en masse* to entrap them on the surface of inverted poured agar plates and thus make isolations.

APPEARANCE OF THE DISEASE

Ciboria carunculoides, in common with many other members of the genus *Ciboria,* is a gynicolous species. In some instances only a few of the individual drupelets composing the syncarp may be involved and in others essentially all drupelets are stromatized. The common name, "popcorn disease," is unusually appropriate for this sclerotial disease for the reason that each mature stroma (sclerotium) bears a striking resemblance in size and shape to a grain of popcorn (FIG. 1).

Infection occurs at a time when mulberries come into flower. This conclusion was reached as the result of direct microscopic examination by Siegler and Jenkins (1923), and is supported indirectly by the fact that in nature the apothecia reach maturity and ascospores are forcibly discharged at this time. The disease is not evident, however, until three or four weeks after anthesis. It may be noted then, that some of the drupelets are larger than

FIG 1 Popcorn disease of mulberry

the remainder, and that sticky, grayish, columnar extrusions are prominently present at the tips of these affected drupelets (FIG. 3). Soon thereafter the sepals of healthy fruits are becoming fleshy whereas diseased ones remain firm and corneous. These differences become more marked as the time approaches for normal fruits to ripen. Mature stromatized drupelets are always considerably larger than healthy ones and are always grayish; *i.e.*, they never assume the color of mature normal drupelets.

The forcible expulsion of ascospores and their dissemination by convection currents is an efficient means of scattering the inoculum (ascospores), as shown by the distribution of diseased fruits throughout the trees. During each of the three seasons covered by these studies all the mulberries borne on the row of trees under observation were severely attacked. These trees are approximately 30 feet tall. Fruits borne on the lowermost branches were neither more nor less abundantly parasitized than those borne on the topmost branches. The abscission of diseased fruits occurs in late June and early July; *i.e.*, at the same time that the healthy ripe fruits are being shed from disease-free trees growing a few blocks away.

MORPHOLOGY AND DEVELOPMENTAL HISTORY OF THE PATHOGEN

Ciboria carunculoides, in common with all other members of the genus, lacks a conidial stage. Its developmental cycle consists of two phases or stages, a sclerotial and an apothecial. Its sclerotial stage functions for hibernation and for the initiation and nurturing of developing apothecia. The apothecial stage (FIG. 2) functions for reproduction and dissemination. The former stage is initiated in the vicinity of Durham, N. C., from ascospores that are discharged during late March and early April. The latter is initiated about a month later. Each stage requires for its complete development a period of approximately eleven months duration.

Sclerotial stage: The sclerotia are stromatic structures that are constituted both of fungus and of suscept tissues. These stromata have their beginning at the time of flowering. From sections of flowers it may be noted, as was done by Siegler and Jenkins (1923), that hyphae arising from ascospores ramify throughout

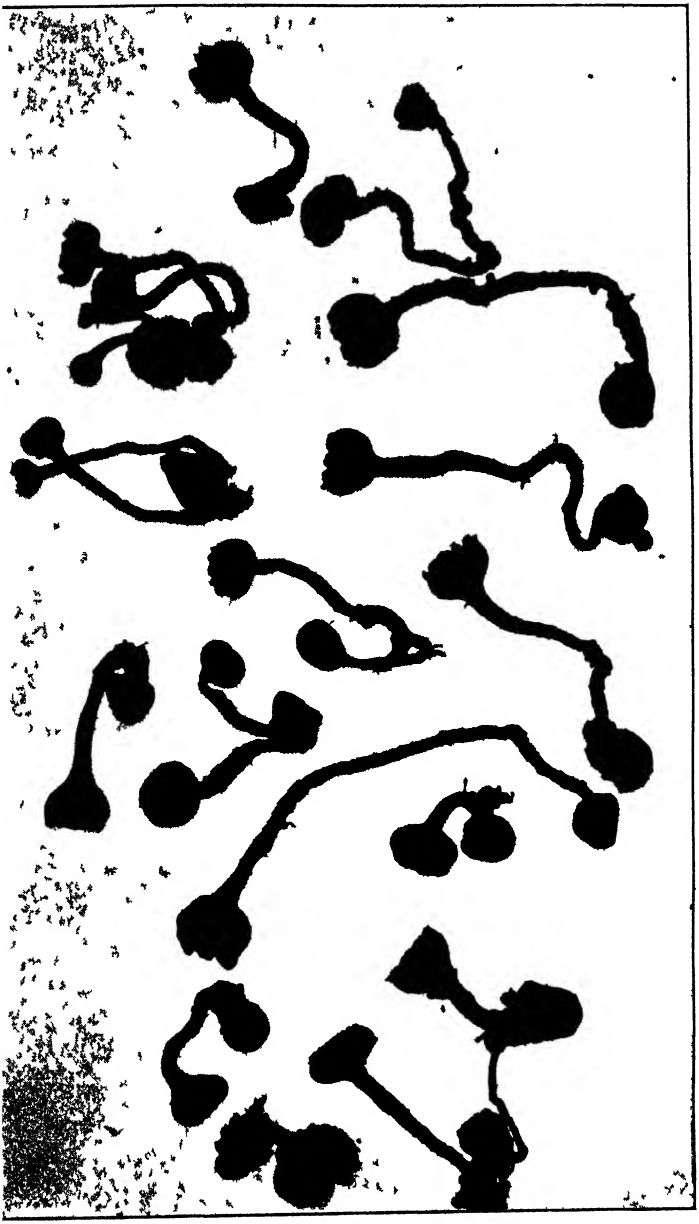

FIG 2 *Ciboria carunculoides*

the tissues of the stigma and style (FIG. 4 A). It is not until three or four weeks later, however, that morphologic symptoms are apparent. Then each infected drupelet is larger than normal, is urceolate in shape, grayish white, and of firm texture. As seen under the microscope, the exterior of each stroma is found to consist of the outer tissues of the sepals (FIG. 3). Immediately beneath is an hymenial layer that practically envelops the entire

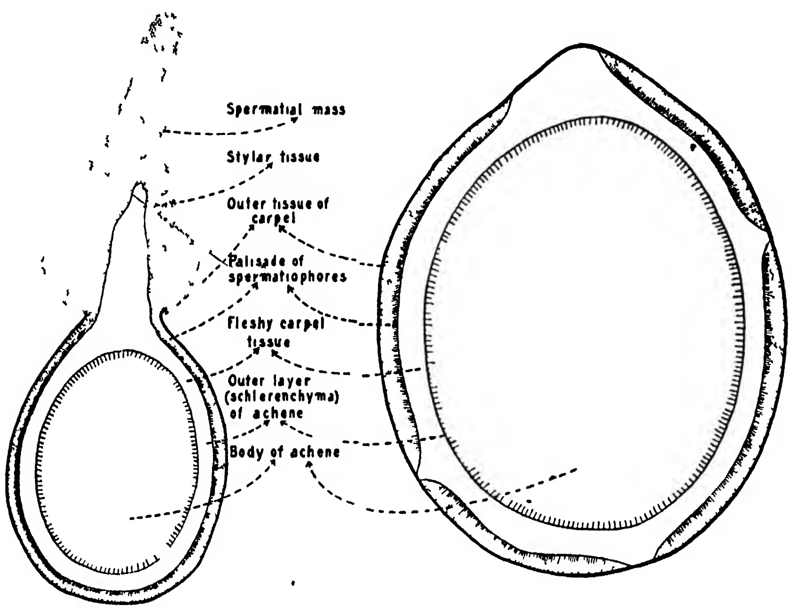

FIG. 3. Popcorn disease of mulberry.

stroma. This layer (FIGS. 3 and 4 C) is constituted of a palisade of spermatiophores and interspersed archicarps. Globular spermatia are budded *seriatim* from the apices of the spermatiophores, and are extruded in a gelatinous matrix as a collar around the remnants of the style and stigma. They are produced in such profusion as to form columns one to two millimeters in height (FIG. 3). The mycelium appears to course at will, both intracellularly and intercellularly, throughout the style and stigma tissues (FIG. 4 A), and is for the most part densely compacted and intercellular within the basal portions of the carpels (FIG. 4 B).

The layers of sclerenchyma that constitute the outer portion of the achene are quite free from invasion (FIGS. 3 and 4 D), and

consequently remain quite unchanged even in mature sclerotia. The presence of sclerenchyma makes difficult the preparation of satisfactory paraffin sections. All tissues on the interior of the achene are densely and compactly occupied by intracellular fungus tissue (FIG. 4 E). Here each hyphal element is invested with a gelatinous membrane.

Intercellular hyphae sparsely occupy the bracts that subtend each drupelet. These bracts seem never to be destroyed and they are never incorporated into the sclerotia. Early in June the grayish sclerotia will have become ellipsoidal and 3 to 5 millimeters in longest diameter (FIG. 3). They may then shatter singly or the entire syncarp *in toto* may fall away. The fallen sclerotia soon become black, are of a corneous consistency, and remain unchanged in size during dormancy. Such sclerotia as are not destroyed by biological or other agencies during the fall and winter produce apothecia in late March and April of the following year.

As a first step leading to the breaking of dormancy the sclerotia swell and may become several times their size while dormant. Soon thereafter one or two stipitate apothecia arise from each swollen sclerotium (FIG. 2). Efforts to break dormancy of stored sclerotia prematurely, by modification of temperature and moisture conditions, have been unsuccessful.

Apothecial stage: As previously stated, apothecial development is initiated about a month after the young fruits have been inoculated. In all likelihood the developmental pattern in essential features is like that described by Drayton (1934) for *Sclerotinia Gladioli* (Massey) Drayton. From the spermatiophores arranged in palisade fashion, spermatia are acrogenously abstricted throughout a period of approximately three weeks duration. Slender deeply-staining hyphae, that are indicated to be tips of archicarps (trichogynes), are interspersed among the spermatiophores, and they extend well above them. Spermatia have been found attached to these trichogyne-like structures, but it has not been possible to determine whether fusion of spermatium with trichogyne actually occurs. It seems very probable, in the light of knowledge of other disc fungi, that they do and that fertilization follows. During the entire period thereafter until the following spring, little further change occurs. Then follows within a brief period the swelling

of sclerotia, protrusion of stipes, and expansion of the discs. Mature cupulate discs are 4–12 mm. in diameter and brown in color. The cylindrical stipes are straight or flexuous, attenuated downward, 15–42 mm. long, and brown. The cylindrical asci measure 104–123 × 6.4–8 μ. The ascospores are reniform, each with a peculiar structure, the caruncle, on the concave side, and they measure 6.4–9.6 × 2.4–4 μ. The filiform paraphyses are usually branched and septate (FIG. 4 G).

The genus *Ciboria,* as delimited by Whetzel in unpublished notes, has the following characteristics: The stromata (sclerotia) are black or brown, andricolous or gynicolous, and mummioid. The spermatiophores form a mantle around the developing sclerotium, and the spermatia are globose or ovate, hyaline or faintly brownish in mass. A conidial stage is wanting. The apothecia are cupulate to shallow saucer-shaped, becoming flat expanded or even reflexed convex, and are some shade of brown, especially vinaceous brown. They are small to medium in size. The ascospores are ellipsoid, inequilateral, 1-celled, hyaline, smooth or adorned with stipples or depressions.

The type species is *Ciboria Caucus* (Reb.) Fuckel, Symb. Myc. 311, 1869.

Manifestly the mulberry pathogen should be referred to *Ciboria* consequently an emended brief description of it, together with essential notes on exsiccati, follows:

Ciboria carunculoides (Siegler and Jenkins) Whetzel, comb. nov.

Stroma (sclerotium) consisting of closely compacted hyphae with thick gelatinous walls together with remnants of the fleshy sepals and of the ovarian tissues; urceolate, when young, enclosed by a whitish outer membrane of the calyx, 3–5 mm. diam.; globose to subspherical and black when mature, 7–10 mm. diam. Rind constituted of several layers of dark brown cells. Medulla of densely interwoven hyphae, both inter- and intracellular.

Spermatia hyaline, ovate, 2–4 × 2–2.3 μ, av. 2.8 × 2.5 μ (Siegler and Jenkins), 3.6 × 2.4 μ (Whetzel), produced successively from the tips of slender, obclavate spermatiophores which form a continuous hymenium over the surface of the developing sclerotium. Spermatia exude in waxy threads or masses through the tip of the membrane that encloses the developing sclerotium.

Apothecia one to several from a sclerotium; disc cupulate to subcupulate, 4–12 mm. diam.; snuff brown within, Prout's brown without. Stipe cylindrical flexuous, smooth with tufts of anchoring rhizoids, attenuated downwards, 15–42 mm. in length by 1.5 mm. in diam., Prout's brown. Asci cylindrical to cylindro-clavate,

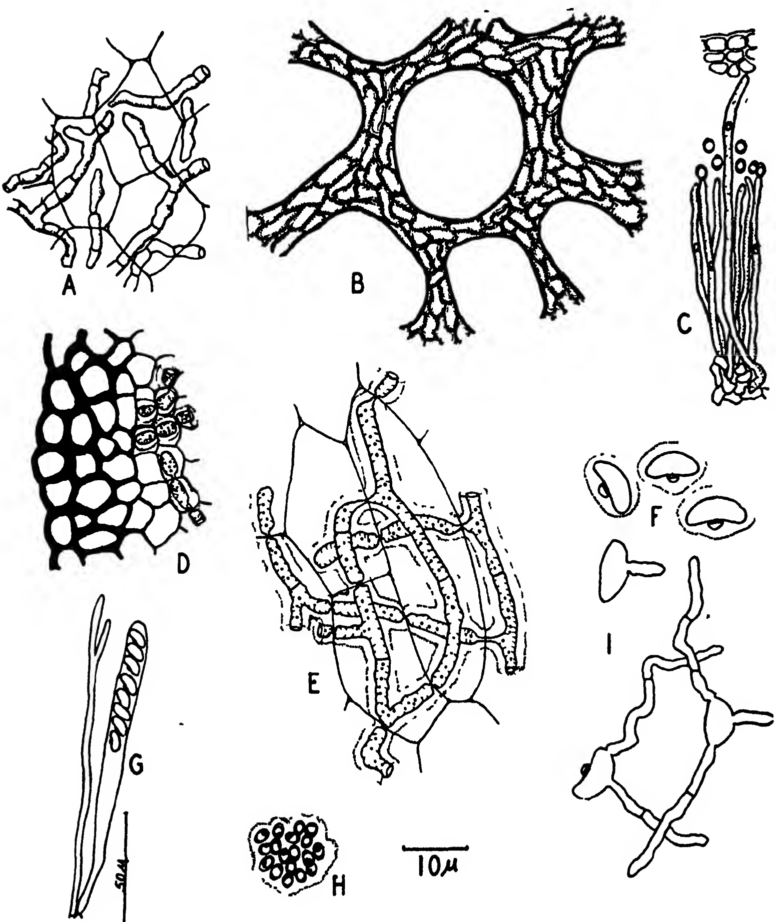

FIG. 4. *Ciboria carunculoides.*

104–123 × 6.4–8 μ, av. 117 × 7 μ, 8-spored. Ascospores uniseriate, reniform, hyaline, 6.4–9.6 × 2.4–4 μ, av. 7.6 × 3.1 μ, with two bodies constituting the caruncle on the concave surface; *i.e.*, the one more or less rhombic as seen from above, 2 × 4 μ, and the other adjoining it, more or less hemispherical, 3 μ in longest diam. Paraphyses filiform to cylindro-clavate, simple or branched, usually septate, 94–128 × 1.8–2 μ.

On fruits of cultivated *Morus alba* L.

Distribution: [1] Alabama, Arkansas (Dunegan and Allen, 1939), Georgia, Florida, Louisiana, Mississippi, North Carolina and South Carolina (Jenkins and Siegler, 1938), and Texas.

Type specimen: Collected by E. A. Siegler, at Scranton, S. C., April 4, 1922; deposited in the Mycological Collections, U. S. Dept. Agr. Duplicate (apothecia), Cornell Univ. Plant Path. Dept. (C. U. P. P.) No. *11810*.

Icones: Siegler and Jenkins, Jour. Agr. Res. **23**: text-fig. 1, and Pls. 1 and 2, 1923.

Other specimens examined: C. U. P. P. No. *33598* (apothecia and sclerotia), apothecia developed in Washington, D. C., by Jenkins, from sclerotia collected in type locality, March 21, 1923; No. *34072* (apothecia). Apothecia developed in Washington, D. C., by E. A. Siegler, from sclerotia collected at Scranton, S. C., March and April 1924 (Myc. Coll. U. S. D. A. No. *68334*); No. *33599* (young sclerotia), Meridian, Miss., June 6, 1927, collected by L. D. Walker; No. *33600* (apothecia), Clemson College, S. C., June 1928, collected by L. M. Fenner; No. *33939* (young sclerotia), Durham, N. C., May 1944, collected by F. A. Wolf.

According to Dr. Anna E. Jenkins the Mycological Collections, U. S. Dept. Agr. contains a specimen on which Orton based his original study labelled "*Spermatomyces Mori* Orton, on *Morus*, Sylvester, Ga., Apr. 29, 1903, Orton," and another from the Herbarium of C. L. Shear labelled "*Sclerotinia carunculoides*, on fruit of mulberry, *Morus*, Delchamps, Ala., coll. L. J. Delchamps, May 1902."

Abundant specimens of sclerotia and apothecia from Durham, N. C., have been deposited in the Farlow Herbarium, Harvard University, in the Herbarium of the New York Botanical Garden and in the Herbarium of the Department of Plant Pathology, Cornell University.

Cultures: Potato dextrose agar, agar enriched by inclusion of green mulberry fruits, and sterilized mulberry fruits alone have

[1] Records of collections are contained in Plant Disease Reporter **8**: 129, 1924; **10**: 12, 1926; **15**: 68, 101, 1931; **19**: 61, 1935; and in Suppl. **20**: 117, 1922; **28**: 375, 1923; **47**: 281, 1926; **52**: 93, 1927; **81**: 88, 1931; **96**: 173, 1936; **119**: 182, 1940; **128**: 311, 1940; **131**: 48, 1941.

been employed as media. Tissue plantings from sclerotia have been made at various times throughout the year. No particular difficulties attend isolation except that the organism does not grow rapidly on any of these media. The colonies are white and floccose but lack distinctive features except that sclerotial aggregates may form after approximately a month. Such sclerotia have not been induced to form apothecia however.

GENERAL CONSIDERATIONS

There are a number of points regarding *Ciboria carunculoides* that seem worthy of special attention. Not the least among these is the gelatinous envelope that so prominently invests hyphal elements within sclerotia and ascospores. The senior author has noted that ascospores of most (presumably all) species of Sclerotinaceae possess a gelatinous covering which is lost if specimens are dried or are preserved in fluids. Seemingly no one has directed attention to such envelopes nor have they been illustrated and described in any accounts that have come to the notice of the junior author. Interestingly the ascospores of *Monilinia fructicola* (Wint.) Honey (*Sclerotinia fructicola* (Wint.) Rehm), occurring on plums, are found to have very prominent envelopes. This gelatinous membrane, in the case of *C. carunculoides*, is strikingly apparent while the ascospores are still within the asci and even after they have been freshly liberated. It is not present in preserved specimens nor can the caruncles be found after preservation. The fact that both structures disappear during preservation may be interpreted to indicate that they are of the same nature and that the caruncles may function in gland-like fashion to generate the envelope.

Undoubtedly the gelatinous covering of ascospores serves this fungus in two ways that are essential for its existence: (a) it causes the ascospores to adhere to the suscept and (b) it both retains and supplies moisture during germination. Without this device infections might be limited to periods of high relative humidity, whereas with an ever-available supply of moisture, germination of ascospores and initiation of infection need not be inhibited even during weather when low relative humidities prevail. The increase in size of sclerotia, which occurs with breaking of dor-

mancy shortly before the expansion of apothecia, is not a result of growth but of swelling of fungal cells from absorption of moisture by the gelatinous coating. The sclerotia thereby become water storage reservoirs. Their water supply becomes useful for conversion of food reserves and for maintenance of turgor during the critical period of ascospore expulsion. In the light of these interpretations, therefore, gelatinous membranes constitute an adaptive device of great ecologic significance for *C. carunculoides*.

Attention may well be directed to pecularities in the range of this fungus. It is apparently restricted to the southern parts of the United States (Jenkins and Siegler, 1938) although its host, *Morus alba*, indigenous to China and Formosa, has been widely planted throughout the eastern United States from Canada to the Gulf of Mexico. Why has *C. carunculoides* not appeared farther northward? Its restricted range becomes the more puzzling since most of the known species of *Ciboria* have been collected only in the colder regions of the North Temperate Zone. If *C. carunculoides* is indigenous to the southern United States, how could so striking a fungus have been overlooked by such mycologists as Earle, Atkinson, Carver, and Tracy, who collected so assiduously during the latter part of the 19th century in the region in which this organism is known to occur? It seems a reasonable presumption that this fungus must have been introduced quite recently from China.

Evidence that it is native to China and was introduced into the United States is, however, not convincing. As bearing on introduction from the Orient, consideration should be given to the possible identity of *C. carunculoides* and *C. Shiraiana*, the latter having been described as *Sclerotinia Shiraiana* by Hennings (1900) from specimens on mulberry fruit sent from Japan by Shirai. It can scarcely be questioned, from the records by Teng (1934, 1939) and by Tai (1937) in China, and by Sawada (1937) in Formosa, that *C. Shiraiana* occurs in Asia. Incidentally Sawada records the occurrence of *C. Shiraiana* both on *Morus alba* and *M. acidosa* Gr. It should be remembered, however, that collectors throughout Asia have failed to recognize *C. carunculoides* among their specimens. Siegler and Jenkins (1923), after examining specimens sent to them by Shirai, were convinced that

C. Shiraiana and *C. carunculoides* are specifically distinct. They pointed out that the drupelets are collectively merged into one stroma that simulates a mumified fruit in the former species, while in the latter each drupelet is separately stromatized. Moreover the ascospores of the former are ovoid to ellipsoid and not reniform as in the latter. According to Teng (1939, p. 171) the asci of *C. Shiraiana* are 140–170 × 8–11 μ and the ascospores are 11–15 × 4.5–6 μ. These measurements are in excess of those given in the original description by Hennings. Moreover the measurements both of Hennings and of Teng show that the asci and ascospores of *C. Shiraiana* are larger than those of *C. carunculoides*. On the other hand the external characteristics of apothecia of the two are strikingly alike. Nevertheless there can be little doubt that the two species are distinct. Judging from Prof. Whetzel's notes, he was of this opinion and was convinced that the Asiatic mulberry fungus belongs to *Ciboria* and should become **Ciboria Shiraina** (Hennings) Whetzel, comb. nov.

SUMMARY

A developmental study has been made of a disc fungus that attacks the fruits of *Morus alba*. From the results obtained, the organism is transferred from *Sclerotinia* to *Ciboria*, and is assigned the binomial *Ciboria carunculoides* (Siegler and Jenkins) Whetzel.

This fungus possesses a sclerotial phase and an apothecial phase, but lacks conidia. Its ascospores, which are forcibly expelled, lodge on the stigmas and constitute the inoculum for initiation of infection at the time of flowering. As a result each drupelet of the aggregate fruit may become transformed into a separate sclerotium.

Sclerotia are composed both of fungus and of suscept tissues and have somewhat the appearance of grains of popcorn.

Apothecia for the succeeding year are initiated in the spring about a month after discharge of ascospores. They originate from elements of a mantle that occurs immediately beneath the outer tissues normally destined to become the fleshy portion of the mulberry fruits. This mantle completely invests the young sclerotium and consists of spermatiophores with interspersed archicarps.

The spermatia are produced in such abundance as to be extruded in a column at the tip of each sclerotium.

Sclerotia fall to the ground during mid-summer, become black. and remain dormant until the following spring. Then each bears one or two apothecia. The breaking of dormancy is first indicated by increase in size of sclerotia. Increase in size is accounted for by the presence of a gelatinous covering on the sclerotial hyphae. This gelatinous envelope absorbs water, causing the sclerotia to swell, and also functions to maintain turgor during expulsion of ascospores.

Ascospores possess thick gelatinous envelopes which cause them to adhere and provides moisture for germination.

An Asiatic fungus, *Sclerotinia Shiraiana*, parasitic on mulberry appears to be distinct from *C. caruncuIoides* but properly belongs in the same genus. It is herein transferred to *Ciboria Shiraiana* (Henn.) Whetzel.

CORNELL UNIVERSITY,
ITHACA, N. Y.,
AND
DUKE UNIVERSITY,
DURHAM, N. C.

EXPLANATION OF FIGURES

FIG. 1. Stromatized fruits of mulberry, the sclerotial phase of *Ciboria caruncuIoides*. Each drupelet may become a sclerotium.

FIG. 2. Apothecial phase of *C. caruncuIoides*, arising from sclerotia.

FIG. 3. Diagrammatic representations to the same scale of stromata and their components in section. At the left a young sclerotium when first the fruits are observed to be diseased; at the right a sclerotium at the stage when sclerotia are shattering and falling to the ground.

FIG. 4. Detailed sketches of parts shown in figure 3. All figures except G are drawn to the same scale (near H): A, The mycelium courses through the thin-walled tissues of style and stigma; B, Within the fleshy tissue of the carpel the mycelium is mainly intercellular; C, Palisade of spermatiophores beneath the outer carpel tissues. An occasional deeply-staining hypha, presumably the upper portion of an archicarp, extends beyond the spermatiophores; D, The sclerenchyma tissue at the exterior of the achene is quite free from invasion. The cells beneath are occupied by hyphae with gelatinous sheaths; E, Tissue from the central portion of the achene occupied by sheathed hyphae; F, Freshly discharged ascospores of *C. caruncuIoides;* G, Ascus and branched paraphysis; H, Mass of spermatia embedded in a mucoid matrix, from the column extruded around the style and stigma; I, Germinating ascospores.

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A LEAF SPOT OF TALL FESCUE CAUSED BY A NEW SPECIES OF CERCOSPORA [1]

JOHN R. HARDISON [2]

(WITH 1 FIGURE)

During an investigation of grass diseases in Kentucky in 1942–44 a leaf spot was collected on *Festuca elatior* var. *arundinacea* (Schreb.) Wimm. caused by a fungus tentatively identified as *Cercospora* sp.[3] Specimens were sent to Dr. Charles Chupp, Cornell University, who replied that the fungus was distinct from any of the species of *Cercospora* described on the Graminaceae, especially by its distinctly acicular and long conidia and also by its almost straight conidiophores. Dr. Chupp very kindly suggested the name *Cercospora Festucae* Hardison and sent detailed morphological notes which largely represent the description below.

Cercospora Festucae Hardison, sp. nov.

Maculis ovatis vel elongatis, 0.5–4 mm. longis, centro cinereis, margine purpurea, absque stromatibus vel cellis paucis brunneis; fasciculis cum 2–8 conidiophoris divaricatis; conidiophoris prope bases pallidis vel mediocriter olivaceo-brunneis, pallidioribus et aliquando angustus ad apicibus, parce septatis, rarus geniculatis, prope rectis, non-ramosis, apicibus rotundatus vel subtruncatis, 3.5–5 × 50–800 μ; conidiis hyalinis, acicularibus, curvatis vel undulatis, indistincte pluriseptatis, infra truncatis, supra acutis, 2–4 × 40–300 μ.

In foliis vivis *Festucae elatiorae* var. *arundinaceae*. Specimen typicum legit J. R. Hardison in foliis *Festucae* prope urbem Lexington, Kentucky, July, 1944.

[1] Coöperative investigations between the Division of Forage Corps and Diseases, Bureau of Plant Industry, Soils and Agricultural Engineering, U. S. Department of Agriculture, and the Oregon Agricultural Experiment Station. Published with the approval of the Director of the Oregon Experiment Station as Tech. Paper No. 455. Contribution of the Department of Botany.

[2] Associate Pathologist, Division of Forage Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

[3] Hardison, John R. Observations on Grass Diseases in Kentucky, Sept. 1942–44, and a Preliminary Check List. Plant Dis. Reptr. **29** (3): 76–85. 1945.

Leaf spots oval to elongate, 0.5–4 mm. in length, gray center, purplish border; stromata none or a few brown cells; fascicles 2–8 divergent stalks; conidiophores near base pale to medium olivaceous brown, paler and sometimes more narrow toward the tip, sparingly septate, rarely geniculate, almost straight, not branched, rounded to subtruncate tip, 3.5–5 × 50–800 μ; conidia hyaline, acicular, curved or undulate, indistinctly multiseptate, base truncate, tip acute, 2–4 × 40–300 μ.

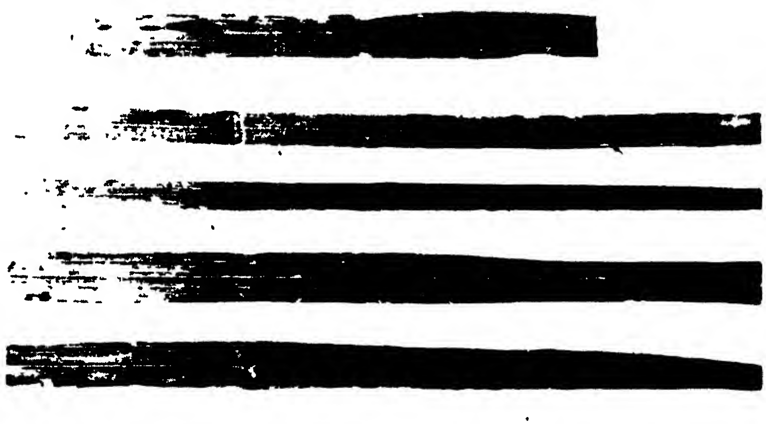

FIG. 1. Habit of *Cercospora Festucae* on leaves of *Festuca elatior* var. *arundinacea.*

In living leaves of *Festuca elatior* var. *arundinacea.* Type specimen collected in the vicinity of Lexington, Kentucky, July 1944, John R. Hardison.

Type material has been deposited in the Mycological Collections of the Bureau of Plant Industry, Beltsville, Maryland (*B.P.I. 71419*) and in the herbarium of Oregon State College (*O.S.C. 15,094*).

The occurrence of a *Cercospora* leaf spot on tall fescue, *F. elatior* var. *arundinacea,* is of considerable interest since very few diseases have been observed on this grass. The effects of the disease have been mild thus far. Typical symptoms are shown in figure 1. It will be interesting to see if it increases in severity or in occurrence.

A considerable number of plants of common meadow fescue, *Festuca elatior* L., were growing nearby, and none of these were observed to be infected. However, several plants intermediate in type between *F. elatior* and *F. elatior* var. *arundinacea* were infected, and possibly *F. elatior* will be found to be susceptible.

OREGON AGRICULTURAL EXPERIMENT STATION,
CORVALLIS, OREGON

A NEW SPECIES OF CEPHALOSPORIUM CAUSING PERSIMMON WILT

BOWEN S. CRANDALL [1]

(WITH 1 FIGURE)

In the studies of the wilt disease of persimmon (1) in the Southeastern States a fungus was isolated from the wood of wilting persimmons and found fruiting in abundance on wilt-killed trees. It is a species of *Cephalosporium* (FIG. 1).

A search of the literature disclosed no member of the genus *Cephalosporium* resembling the persimmon wilt fungus. The literature on diseases of persimmon and ebony contains no reference to a disease caused by a *Cephalosporium*. In the course of the investigation of this disease no perfect stage has been found, nor has it been possible to produce one by intercrossing all available isolates collected during the scouting activities from all parts of the known range of this fungus. Little variation has thus far been observed between any of the isolates, regardless of their origin. For this reason, in the description that follows, all measurements are based on the isolates of the fungus from the point of original discovery in Tennessee. The specimen and culture, No. D-27, on which the description is based, have been designated as the type and deposited in the Mycological Collections of the Bureau of Plant Industry, Soils, and Agricultural Engineering, U. S. Department of Agriculture. The fungus causing the wilt disease is here described as a new species. Description of the hyphae is based on the growth of the fungus on 2 per cent malt agar.

Cephalosporium Diospyri sp. nov.[2]

Mycelium in culture at first appressed and watery, later faintly pinkish white and fluffy; aerial mycelium often composed of many

[1] Formerly Assistant Pathologist, Division of Forest Pathology, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration; now Pathologist, Office of Foreign Agricultural Relations, U. S. Department of Agriculture.

[2] The Latin description was prepared by Edith K. Cash, Associate My-

parallel adherent hyphae that are hyaline, vesiculose, sparsely branched, 3.8 μ to 7.6 μ in diameter with indistinct septations; conidiophores hyaline, simple, non-septate, 1.5 μ to 3.5 μ wide at the base, gradually tapering to the tip, 10 μ to 60 μ long, mostly arising at right angles from the hyphae; conidia hyaline when viewed singly but orange-pink [3] in mass, continuous, ovate or ellipsoid to cylindric, the ovate predominating in young cultures and in nature, 2.7–11.7 μ × 1.8–5.4 μ, but 94 per cent 2.7–4.5 μ long, produced acrogenously and forming small globose heads averaging 10 μ in diameter, which break up readily in air or water.

Mycelium in culturis primo appressum aquosumque, deinde pallide roseolo-album et lanosum; mycelium aerium ex hyphis multis, adhaerentibus, hyalinis, vesiculosis, parce ramosis, 3.8–7.6 μ in diam., indistincte septatis saepe conpositum; conidiophora hyalina, simplicia, eseptata, e basi 1.5–3.5 μ lato apicem versus gradatim attenuata, 10–60 μ longa, plerumque ad angulos rectos ex hyphis oriunda; conidia singula hyalina, in massis aurantio-rosea, continua, ovata vel ellipsoideo-cylindrica, in culturis juvenilibus et in natura praecipue ovata, 2.7–11.7 μ longa, 1.8–5.4 μ lata, maxima ex parte (94 per centum) 2.7–4.5 μ longa, acrogena, in capitulis globosis circum 10 μ in diam. in aquo et aere mox dissolventibus aggregata.

Cephalosporium Diospyri differs from most other described members of this genus in its abundant production of orange-pink spores and in having a faint pink color in culture. Two species, *C. acremonium* Cda. and *C. carpogenum* Ruehle, are described as being faintly pink in culture. *C. acremonium* Cda., as described by Corda (2), was given such wide limits that it would include almost any *Cephalosporium*. Reddy and Holbert (6) summarized the later concepts of this species, which are in general agreement in giving to this species a spore size averaging 4.5 μ × 1.3 μ. The isolates of *C. acremonium* Cda. with which they worked had a spore size of 3.6 μ × 1–1.8 μ and an average size of 4.3 μ × 1.3 μ. *C. carpogenum* Ruehle (8) is described as having spores 4–8.5 μ × 1.4–2.8 μ. *C. Diospyri* may be differentiated from either *C. acremonium* or *C. carpogenum* by its more ovoid spores and by the larger size of the ellipsoid spores present.

cologist, Division of Mycology and Disease Survey, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.

[3] Color according to Ridgway (7).

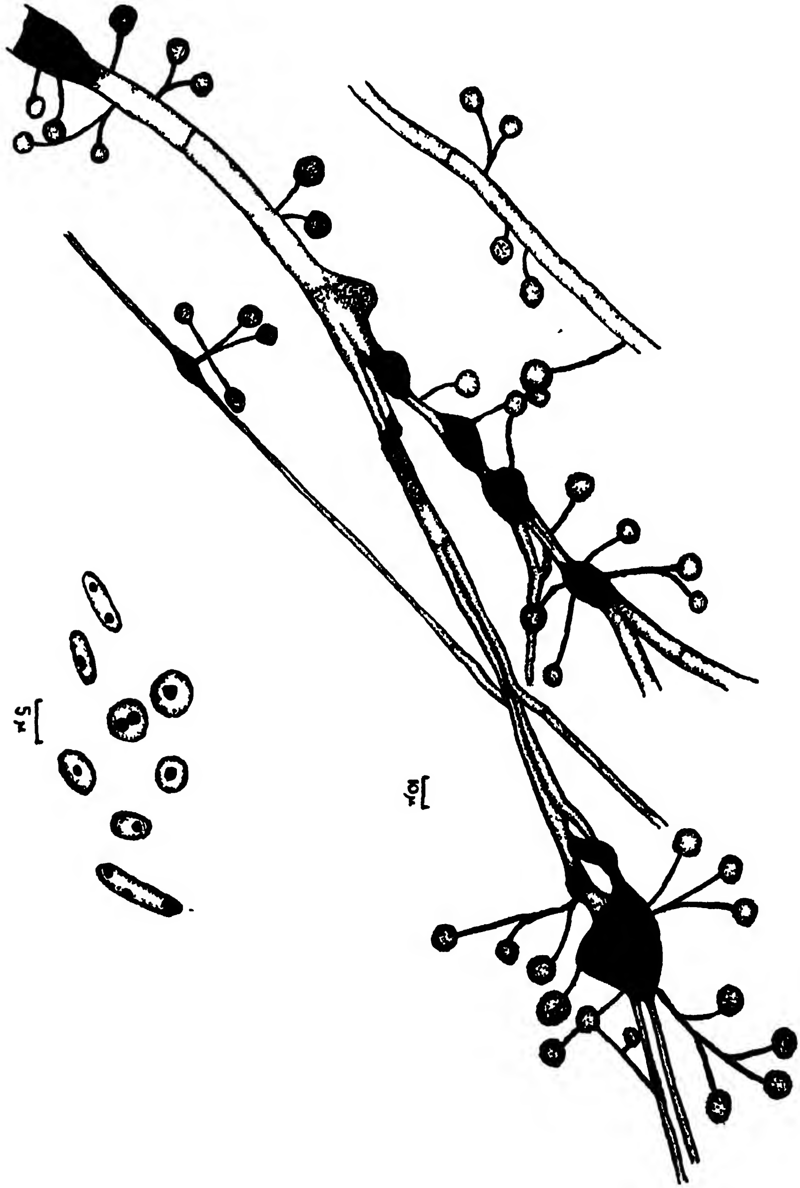

FIG. 1. A, Hyphae and conidiophores; B, Conidia of the persimmon wilt *Cephalosporium*.

The fungus has been found in nature on the American persimmon (*Diospyros virginiana* L.) on which it causes a serious wilt disease; on the Oriental persimmon (*D. Kaki* L. f.), which is nearly immune but is often killed when grafted on susceptible *D. virginiana* roots.

By inoculation it has been found that *D. ebenaster* Retz., a widely cultivated East Indian species of which the material came from Mexico, is highly susceptible; *D. texana* Scheele of Texas and Mexico is fairly susceptible; *D. lotus* L. used as grafting stock in the Orient is very slightly susceptible. Inoculations have failed on *D. Rosei* Standley of Mexico, *D. montana* Roxb. of India, and *D. discolor* Willd. from the Philippines.

To date the disease is known to occur in the United States in Texas (**5**), Tennessee, Mississippi, Alabama, Georgia, Florida, South Carolina, and North Carolina (**3**, **4**).

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PRESERVATION OF MOLDS BY THE LYOPHIL PROCESS

KENNETH B. RAPER [1] AND DOROTHY F. ALEXANDER [2]

(WITH 3 FIGURES)

Subsequent to the establishment of the four Regional Research Laboratories by the Department of Agriculture, a large collection of industrially important microörganisms was assembled at the Northern Regional Research Laboratory as an integral part of the research program of the Fermentation Division. From the outset it was recognized that this collection could be of the greatest possible value only if variation in the organisms was kept at an absolute minimum. It was likewise recognized that the routine labor involved in propagating individual cultures should be reduced as much as possible in order that a large and varied collection could be maintained. The accomplishment of both objectives through preservation of cultures by some type of vacuum desiccation from the frozen state appeared as a real possibility. The experience of numerous bacteriologists (Shackell, **1909**; Hammer, **1911**; Rogers, **1914**; Swift, **1921**, **1937**; Brown, **1932**; Elser, Thomas, and Steffen, **1935**; and Flosdorf and Mudd, **1935**, **1938**) during the past quarter of a century left little doubt that this method could be successfully used for the preservation of bacterial cultures contained in the collection. Some published reports (Rogers, **1914**; Elser, Thomas and Steffen, **1935**) and other work then known to be in progress (Wickerham and Andreasen, **1942**) likewise indicated that the method could probably be successfully applied to the yeasts. Regarding the molds, however, there were few and fragmentary reports, and these were generally not too

[1] Senior Microbiologist, Fermentation Division.
[2] Junior Microbiologist, Fermentation Division.
From the Northern Regional Research Laboratory, Peoria, Illinois, one of the laboratories of the Bureau of Agricultural and Industrial Chemistry, Agricultural Research Administration, United States Department of Agriculture.

favorable. Bushnell (1941) reported unsuccessful attempts to preserve fungi (identity unstated) by freezing and by subsequent vacuum desiccation. Conant in 1941 (personal communication) reported rather indifferent success. Among the strains tested by Wickerham and Andreasen (1942) were 16 "Dermatophytes and other molds" of which 15 were viable at 12 months. Included in this number were 2 species of *Aspergillus*, 2 of *Penicillium*, various pathogenic species, and some miscellaneous forms.

Despite a dearth of positive evidence it was decided to investigate the possibility of preserving molds by this technique, and to process the entire mold collection if it could be demonstrated that the method was applicable to the fungi. Preparations of a limited number of selected cultures were made during the spring and early summer of 1941. In December of the same year, when the preparations had been stored for approximately 6 months, streak plates made from the dried cultures showed neither appreciable loss of viability nor apparent change in morphological characteristics. While these results were in no sense conclusive, they were at least indicative, and the contemplated program of mass freezing and drying was pushed through to completion as rapidly as possible. By July 1, 1942, the entire collection of 1850 molds, more than 900 yeasts, and approximately 400 bacterial cultures then contained in the Collection at the Laboratory had been processed. The present paper is concerned with results obtained with preservation of molds up to the present time and is presented in response to an increasing number of inquiries concerning the practicability and reliability of this method for the preservation of mold cultures. These inquiries have been particularly numerous regarding the preservation of penicillin-producing strains of *Penicillium notatum* and allied species. Special attention will therefore be given to these molds.

FIG. 1. Materials and preparation. A, plate culture of *Penicillium chrysogenum*, NRRL 1951.B25, from which spores (conidia) have been removed; B, platinum loop, 4 mm., used to collect spores; C, spore suspension in sterile beef serum; D, long, thin-necked pipette used for filling lyophil tubes; E, lyophil tubes labeled, containing approximately 0.05 cc. of spore suspension each, ready to be processed; F, completed preparations showing compact chalky pellets of dried, spore-laden serum.

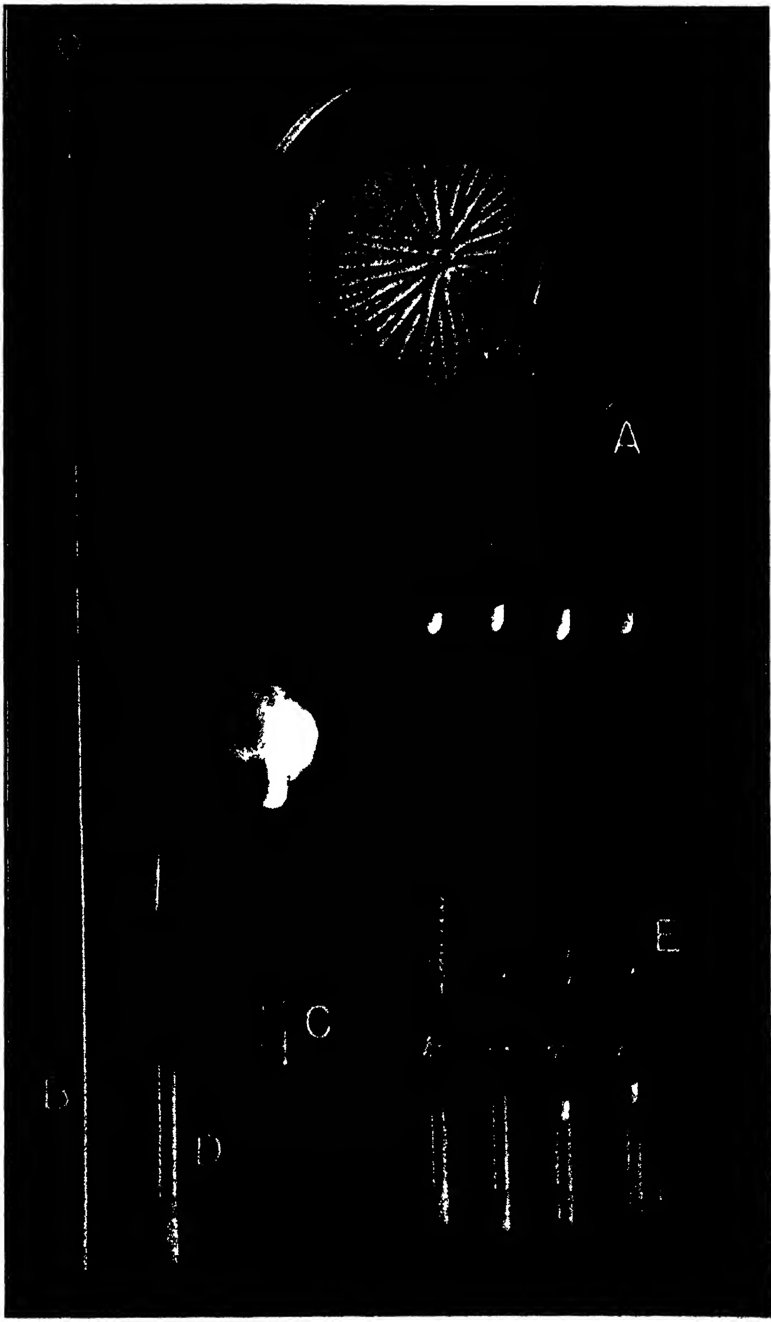

Fig. 1.

APPARATUS AND METHODS

The present report is based upon cultures that were processed on three pieces of lyophil apparatus. Cultures reported as having been maintained in lyophil form for 21 months or more were lyophilized according to the method used by Wickerham and Andreasen (1942) and upon an apparatus of the type described and illustrated by them. Those reported as having been kept in lyophil form for less than 21 months were processed on the apparatus shown in figure 2, which was designed by Dr. L. J. Wickerham and constructed in the mechanical shops of the Northern Regional Research Laboratory. Cultures preserved within the past year have been processed on the table model shown in figure 3. The methods employed were essentially the same for each type of apparatus and will be briefly described in connection with the operation of the portable unit shown in figure 2.

Materials used to prepare the cultures for drying include: (1) plugged and sterilized agglutination tubes; (2) micropipettes made from 10-mm. Pyrex glass tubing; (3) plugged and sterilized lyophil tubes made of 4-inch lengths of 6-mm. Pyrex glass tubing, sealed at one end and lightly fire-polished at the lip; and (4) glass writing ink [3] for marking the tubes.

Cultures were grown, in the usual manner, on Czapek's solution agar or malt extract agar in either test tubes or Petri dishes (FIG. 1 A) for from 1 week to 10 days, or until a sufficient quantity of conidia was produced. Approximately 0.25 cc. of sterile beef serum was placed in an agglutination tube, and spores or conidia were added from the culture to be lyophilized until the resulting suspension was comparatively dense (FIG. 1 C). By means of a micropipette (FIG. 1 D), approximately 0.05 cc. of the suspension was then dispensed into each of four previously labeled, sterile lyophil tubes. The cotton plugs were replaced, and the excess cotton was burned off. The remaining portion of the plug was then pushed down into the tube to a depth of about one-half inch as a precaution against possible contamination during processing, and to prevent the cotton from being drawn up into the apparatus during evacuation (FIG. 1 E)

[3] We have employed successfully a product marketed by the Clay-Adams Co. of New York under the trade name "Gold Seal" Laboratory ink.

The lyophil tubes containing the spore suspension were then attached to the manifold by inserting them in the rubber sleeves shown in figures 2 and 3. The whole manifold, the height of which can be adjusted by a screw-lifting device, was lowered, and the ends of the tubes containing the spore suspension were submerged in a bath of dry ice and methyl cellosolve at a temperature of about — 40° to — 50° C. The small amount of material in the tubes was completely frozen within a few seconds, and evacuation by means of a vacuum pump [4] was begun as soon as this was accomplished. The tubes were then raised above the surface of the bath to a position where the temperature at the level of the frozen suspension was approximately — 10° C.; they were held at this temperature by adjusting the height of the manifold during the drying process.

In the portable apparatus (FIG. 2), as in the smaller apparatus developed by Wickerham and Andreasen (1942), water vapor removed from the frozen preparations is taken up in a column of anhydrous calcium sulfate (Drierite [5]). This column, which is placed between the manifold and the vacuum pump, is provided with two glass stopcocks, one at the lower end, leading to the pump, and another in the rubber hose, leading to each manifold. The column can thus be closed off and the desiccant protected when the apparatus is not in operation. At the end opposite that of attachment to the drying column, each manifold is connected to a single, Bruner-type vacuum gauge by means of a two-way glass stopcock. The two manifolds can be operated simultaneously, or either manifold can be operated alone. Employing both manifolds, a total of 60 preparations can be desiccated in one operation. When the apparatus is fully loaded, desiccation usually requires 1½ to 2 hours.

At the outset, the frozen suspension normally appeared glassy, but, as drying progressed, the mass became chalky in appearance and assumed the shape of a compact, cylindrical pellet. When the pellets appeared completely dry, the tubes were raised to room

[4] Cenco Hi-Vac and Welch Duo Seal pumps (FIGS. 2, 3) have been used successfully.

[5] Trade name of a commercial product marketed by the W. A. Hammond Company, Yellow Springs, Ohio.

temperature, the bath was covered, and drying was continued for half an hour to insure thorough desiccation. The tubes were then sealed off with a Hoke gas-oxygen torch (FIGS. 2, 3).

While we have no evidence that the viability of cultures dried at pressures of 1 to 2 mm of mercury is not satisfactory, drying

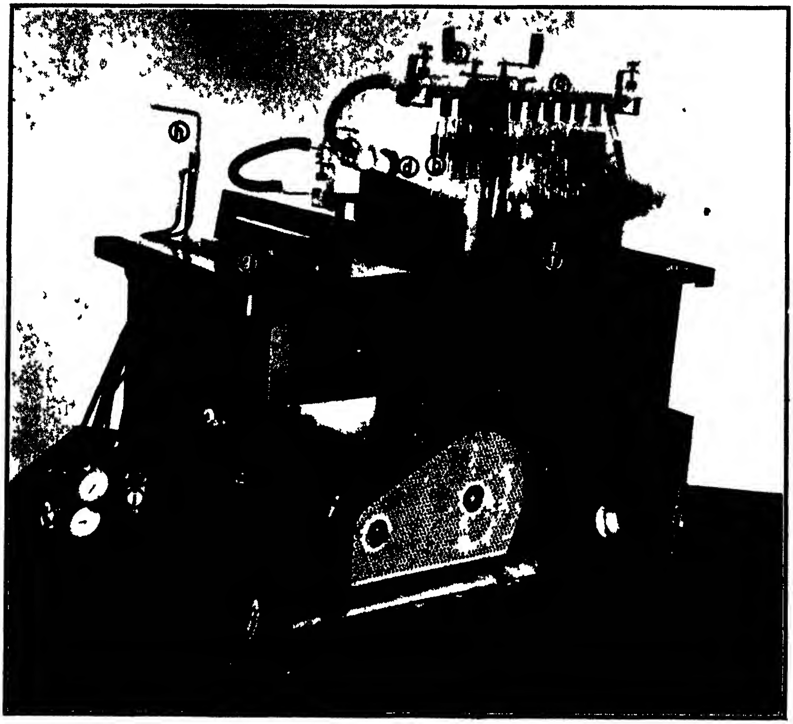

FIG 2 Portable lyophil apparatus, a, manifold, b, lyophil preparations in final stage of drying, c, screw lift for raising and lowering manifold, d, drierite column, e, vacuum pump, f, freezing bath, g, multiple terminal panel for testing evacuation of finished preparations; h, oxygen-gas torch; i, oxygen storage tank

proceeds more favorably when a vacuum between 200 and 500 μ of mercury is maintained.

Twenty-four hours after processing, the lyophil preparations were tested with a high-frequency, spark-coil tester to ascertain the existence of a vacuum in the completed cultures. Any tube which failed to show evidence of a good vacuum was discarded. The four finished preparations of each strain were then placed in

a small, screw-cap vial and were stored in a refrigerator at 3° to 5° C. One of the advantages of lyophil preservations is the saving of storage space; for example, in our trays, which measure 14½" × 12½" × 2½", quadruplicate preparation of 300 separate cultures can be stored.

FIG. 3. Lyophil apparatus, table model. a, manifold; b, Bruner-type vacuum gauge; c, thermometer; d, lyophil preparations in final stages of desiccation; e, Dewar flask containing a water-vapor trap immersed in CO_2-ice and methyl cellosolve; f, vacuum pump; g, insulated freezing bath; h, vacuum tester; i, oxygen-gas torch.

The large apparatus shown in figure 2 possesses several marked advantages over the smaller machine of Wickerham and Andreasen (**1942**): (1) the screw-lifting and lowering device (FIG. 2, C) simplifies temperature control during drying; (2) the apparatus is a portable unit which can be easily moved from one laboratory to another; (3) a stationary pressure gauge makes it possible to check the amount of vacuum during processing; (4) a multiple

terminal panel facilitates the testing of finished lyophilized preparations for the presence of adequate vacuum; and (5) 60 lyophil preparations can be made in one operation.

Besides these advantages, the apparatus under discussion has certain disadvantages. The large number of rubber connections makes it difficult to attain a high degree of vacuum, and the $CaSO_4$ (Drierite) used as a desiccant must be frequently regenerated or replaced. With these two limitations in mind, a third model (FIG. 3) was constructed which has proved highly satisfactory. A single manifold with only 30 outlets is used, and ground glass joints have been inserted as connections wherever this is feasible to further reduce sources of possible leaks. The manifold is supported on a horizontal bar attached to a sliding collar on an upright standard. It is raised and lowered manually and can be clamped into any desired position by means of a bolt with a wing nut. The Drierite column has been replaced by a water-vapor trap which is immersed in a bath of solid CO_2 and methyl cellosolve and can be emptied and reassembled within a few minutes.

In recent months, we have used a modified technique suggested by Dr. Wickerham, involving the continuous immersion of the lyophil tubes during the drying process. The preparations are first submerged in a bath at approximately — 30° to — 40° C., and then sufficient cellosolve at 0° C. is added to raise the temperature to approximately — 10° C. The bath is allowed to warm up gradually but is not permitted to go above 0° C. until the preparations appear completely dry. Finally, the tubes are raised to room temperature, and drying is continued for an additional one-half hour.

To recultivate material preserved in lyophil form, the tube is marked with a file scratch, wiped off with alcohol or some other disinfectant, and broken open. The pellet is then dissolved in a small amount of sterile water or nutrient broth, and the resulting suspension is streaked on a suitable medium and incubated at room temperature for a period of a few days, or until typical colonies develop. New isolations are then made, and the culture may be continued in agar slants or relyophilized within 2 or 3 weeks. Resuspended spores from lyophil preparations may be used di-

rectly for the inoculation of flasks or other small vessels employed in actual fermentation investigations.

VIABILITY TESTS OF SELECTED CULTURES

Using the method described by Wickerham and Andreasen (**1942**) and an apparatus similar to that employed by them, a group of 34 selected cultures were preserved in lyophil form during the spring and early summer of 1941. These cultures can be roughly divided into three groups, namely: Group I: Cultures of industrial importance, including citric acid-producing strains of *Aspergillus niger* (NRRL *67*, *584*, *599*, and *602*); gluconic acid-producing strains of *A. niger* (NRRL *3* and *67*) and *Penicillium chrysogenum* (NRRL *811*); diastatic enzyme-producing strains of *A. flavus* (NRRL *693*), *A. Oryzae* (NRRL *692*), and *Rhizopus delemar* (NRRL *1472*); an itaconic acid-producing strain of *A. terreus* (NRRL *265*); fumaric acid-producing strains of *R. Oryzae* (NRRL *1526* and *1528*); and a d-lactic acid-producing strain of the same species (NRRL *395*). Two strains of the penicillin-producing culture of *P. notatum* isolated by Fleming (NRRL *824* and *1209*) were processed a few months later. Group II: Cultures difficult to maintain by conventional methods of periodic recultivation on agar slants, including such forms as *Mucor Rouxianus* (NRRL *1429*), *Phycomyces Blakesleeanus* (NRRL *1554* and *1555*), *Blakeslea trispora* (NRRL *1718*) and *Aspergillus itaconicus* (NRRL *161*). Group III: Cultures characterized by particularly striking morphological and cultural characteristics, including such forms as *Penicillium claviforme* (NRRL *1002*), *P. islandicum* (NRRL *1038*), *P. vinaceum* (NRRL *739*), a tan-spored mutant of *Aspergillus niger* (No. P-88 B), and others.

For the first group of cultures, the objective was twofold: to determine (1) if industrially important cultures could be preserved by quick freezing and thorough vacuum desiccation, and (2) if cultures so preserved would retain, unaltered, the physiological properties which render them valuable. For the second group, the primary objective was to determine if the period of viability could be prolonged materially, which would increase the usefulness of these forms by reducing the work necessary to keep them viable. With the third group the objective was to determine

TABLE 1

VIABILITY OF LYOPHILIZED PREPARATIONS OF SELECTED MOLD CULTURES TESTED AT INTERVALS UP TO APPROXIMATELY 40 MONTHS

Name	NRRL No.	Date processed	Viability of lyophilized cultures							
			Test No. 1		Test No. 2		Test No. 3		Test No. 4	
			Age in mo.	Viability	Age in mo.	Viability	Age in mo.	Viability	Age in mo.	Viability
Aspergillus flavus Link	484	5/ 5/41	4	+++[a]	26	+++	32½	+++	41	+++
A. flavus Link	693	6/25/41	2	+++	24½	+++	30½	++++	38½	+++
A. itaconicus Kinoshita	161	5/14/41	3½	++	26	++	33½	+	41	+
A. niger van Tieghem	3	5/ 5/41	4	+++	26	+++	32½	++++	41	+++
A. niger van Tieghem	67	5/29/41	3	+++	25½	+++	32½	+++	40½	++
A. niger van Tieghem	328	6/ 4/41	3	++++	25	++++	31½	++++	39½	++++
A. niger van Tieghem	334	5/29/41			25½	++	31½	++	39½	+++
A. niger van Tieghem	584	5/29/41			25½	+++	31½	+++	39½	+++
A. niger van Tieghem	599	5/28/41			25½	+	31½	+	39½	+
A. niger van Tieghem	602	5/29/41	3	+++	25½	+++			39½	+++
A. niger [tan mutant]	P-88B	4/ 8/41	4½	+++	18	++++				
A. Oryzae (Ahlburg) Cohn	692	6/25/41			24½	++++	30½	++++	38½	++++
A. Oryzae (Ahlburg) Cohn	695	6/25/41			24½	++++	30½	++++	38½	++++
A. Sydowi (B. & S.) Th. & Ch.	P-35	6/20/41	2½	++++	24½	++++			38½	++++
A. terreus Thom	265	6/25/41	2	++++	24½	++++	31½	++++	38½	++++
A. terreus Thom	273	6/ 4/41	3	++++	25	++++			39½	++++
Penicillium chrysogenum Thom	811	5/ 7/41	3½	++++	26	++++	32½	++++	40½	++++
P. claviforme Bainier	1002	6/21/41	2½	++++	24½	++++			40	+++
P. islandicum Sopp	1038	6/25/41	2	++++	24½	++++			38½	++++
P. lemoni Sopp	1042	6/25/41	2	++++	24½	++++			38½	++++
P. notatum Westling	1209	10/17/41			20½	++++	26½	++++	36	++++
P. notatum Westling	824	1/ 6/42			18	++++	24	++++	34	++++
P. purpurogenum var. *rubri-sclerotium* Thom	1064	5/ 4/41	4	+++	26	+++	31½	+++	40	+++
P. vinaceum Gilman and Abbott	739	6/21/41	2½	++	24½	+			38½	+
Gliocladium vermoeseni (Biou.) Thom	1752	6/25/41	2	+++	24½	+++			38½	+++
Blakeslea trispora Thaxter	1718	6/19/41	2½	+++	24½	+++	31	+++	39	+++
Mucor Ramannianus Möller	1559	6/15/41	2½	++++	24½	++++	31	++++	39	++++
Mucor Rouxianus (Calmette) Wehmer	1429	6/19/41	2½	+++	24½	+++	31	+++	39	+++
Phycomyces Blakesleeanus (+) Burgeff	1554	6/19/41	2½	+++	24½	+++	31	+++	39	+++
Phyco. Blakesleeanus (−) Burgeff	1555	6/19/41	2½	+++	24½	+++	31	+++	39	+++
Rhizopus delemar (Boid.) Weh. & Hanz.	1472	6/18/41	2½	+++	24½	+++	31	+++	38½	+++
Rhizopus Oryzae Went. & Pr. Geerl.	395	5/ 6/41	4	+++	26	++	32½	+++	40½	+++
Rhizopus Oryzae Went. & Pr. Geerl.	1526	5/ 7/41	4	+++	26	++	32½	+++	40	+++
Rhizopus Oryzae Went. & Pr. Geerl.	1528	5/29/41	3	+++	25½	++	31½	+++	39½	+++

[a] ++++ = excellent viability +++ = good viability ++ = fair viability + = poor viability

if forms preserved by the lyophil method would retain, unchanged, the distinctive morphological characters which distinguish them.

Results obtained in viability tests with these selected cultures are presented in table 1. The first preparations were opened when 2 to 4 months old. Growth was obtained in every case, and, without exception, the resulting cultures were entirely typical of the strains under observation. A limited number of preparations, not recorded in the table, were opened at 5 to 6 months. These likewise appeared wholly normal. It was at this time (December, 1941) that we embarked upon the mass processing of the entire mold collection. With few exceptions, a complete set of the 34 cultures selected for preliminary study was tested for viability at approximately 2 years, again at approximately 31 months, and lastly at approximately 40 months. Growth has been obtained in every case, although in some instances this has been only fair, and in a few cases definitely poor (TABLE 1). In the cases of *A. itaconicus* and *P. vinaceum*, limited growth may have resulted from the low concentration of spores contained in the initial preparations (verified by microscopic examination). In *A. niger*, NRRL *599*, abundant spores were present, and limited growth may have resulted from some factor such as the age of the spores or the degree of final dryness. Subsequent tests with this strain (TABLE 2) failed to substantiate an early belief that certain strains of *A. niger* could not be processed satisfactorily.

No attempt was made to measure quantitatively the number of viable spores in any of the preparations reported in table 1. Any cultures scored "++" (fair) or better, however, could be considered satisfactory from the standpoint of maintaining stock cultures, since such a rating implied the development of a reasonable number of colonies within a period of 3 to 4 days. Only in the case of *Aspergillus niger*, NRRL *599*, *A. itaconicus* (NRRL *161*), and *P. vinaceum* (NRRL *739*) were viabilities dangerously low. The few colonies which developed in each of these cases, however, were entirely characteristic of the strains under observation. It is questionable how much longer parallel lyophil preparations of these strains can be depended upon as reliable stock sources, although there has not been any marked reduction in the number o

colonies developing from progressively older preparations opened during the course of the investigation (TABLE 1).

In all cases where comparative tests have been made, the physiological characteristics of cultures preserved in lyophil form have duplicated those of the same strains preserved in agar slant cultures under optimum conditions. Specific examples will be subsequently noted (pp. 517 to 523).

A comparison of viability of certain of these strains (TABLE 1) in agar slant cultures and in lyophil preparations is of special interest. It is regrettable that we did not retain agar slants of all of the selected strains of the same age as the dried preparations.[6] We believe, however, that enough have been retained to permit a limited comparison and evaluation of the two methods. Agar slant cultures of *A. niger*, NRRL *3* and *67*, yielded viable cultures after 40 and 42 months, respectively; NRRL *602* was viable after 31½ months; whereas NRRL *328*, *584*, and *599* failed to grow at 25 months. *Aspergillus flavus*, NRRL *484*, was viable at 40 months; *A. terreus*, NRRL *273*, at 32 months, and NRRL *265* at 30 months. *Aspergillus itaconicus* failed to grow at 40 months and grew very poorly at 28 months. *Penicillium vinaceum*, *P. purpurogenum* var. *rubri-sclerotium*, and *P. chrysogenum* were viable at 40 months. *P. notatum* (NRRL *821*) showed good growth up to 34 months. *Rhizopus delemar* failed to grow at 15 or 20 months. *R. Oryzae*, NRRL *1528*, failed to grow at 23 months and above, while a second strain of *R. Oryzae*, NRRL *1526*, yielded negative results from a tube culture of 15 months, positive from one of 20 months, and again negative from a still older tube culture. Viable cultures were obtained from tubes of *R. Oryzae*, NRRL *395*, up to 30 months. All agar slant cultures had been continuously stored in a refrigerator at 3° to 5° C. Neither the agar slant cultures nor the lyophil preparations were sufficiently old to justify more than tentative conclusions, but more consistently positive results were obtained from the lyophilized cultures. Results obtained with *Rhizopus Oryzae*, NRRL *1526*, are of particular interest since they illustrate that age alone

[6] Our usual procedure is to retain old agar slants for periods of 6 months to a year after new transplants are made. In exceptional cases they may be retained for longer periods.

is not the determining factor governing viability, but that conditions developing within the individual culture tube are probably responsible. The same conclusion is suggested by the behavior of the several strains of *Aspergillus niger*. In no case did cultures developing from old agar slants appear superior to those developing from lyophil preparations, and it is our considered opinion that the latter method will prove more satisfactory for the preservation of mold cultures in stable form over long periods of time. As is noted in the discussion (p. 523), the lyophil technique possesses certain outstanding advantages quite aside from the anticipated, but still only partially confirmed, extension of viability.

FURTHER VIABILITY TESTS

During the period from January to June 1942, quadruplicate lyophil preparations were made of each of the 1850 different mold cultures which were at that time contained in the Culture Collection. When these preparations were from 19 to 23½ months old, tubes of 140 selected strains representing 128 different species in 44 genera were tested for viability, and the resulting colonies were examined culturally and microscopically. In conducting this survey, an effort was made to include a wide variety of forms in order that the results would provide a reliable measure of the practicality of the lyophil technique as a means of preserving molds. Typical species from all of the major groups of the *Aspergilli* and *Penicillia* were selected, as were also representative species and genera of the Mucorales. In addition, 2 members of the Entomophthorales and 23 miscellaneous forms, representing as many different genera, were included.

The results of this survey are presented in table 2.

Aspergilli: Viable cultures were obtained from each of the strains of *Aspergilli* tested, and, of the 41 strains representing 37 different species, only 5 failed to show good or excellent viability and growth. In every case, the resulting colonies were entirely typical. Microscopic examinations showed conidial heads and other structures to be characteristic of the strains under observation.

The five cultures failing to show good or excellent viability included a strain of *Aspergillus carbonarius* (NRRL *369*), a large-

TABLE 2

VIABILITY OF MOLD CULTURES PRESERVED IN LYOPHIL FORM FOR PERIODS OF FROM 1½ TO 2 YEARS

Name	NRRL No	Age in months	Viability
Aspergillus clavatus Desm.	4	20½	++++[a]
A. giganteus Wehmer	10	20½	++++
A. repens (Cda.) DeBary	17	20½	++++
A. ruber (Brem.) Thom & Raper	55	20½	++
A. Chevalieri (Mang.) Thom & Church	79	20½	+++
A. amstelodami (Mang.) Thom & Raper	94	20	++++
A. umbrosus Bain. & Sart.	121	21	++++
A. niveo-glaucus Thom & Raper	127	21	+
A. echinulatus (Delacr.) Th. & Ch.	131	21	+
A. restrictus Smith	148	21	++++
A. itaconicus Kinoshita	161	20½	+++
A. fumigatus Fresenius	163	21	++++
A. Fischeri Wehmer	181	21	++++
A. nidulans (Eidam) Wint.	187	21	++++
A. rugulosus Thom & Raper	211	21	++++
A. variecolor (B. & Br.) Th. & Rap.	214	21	++++
A. unguis (Em.-Weil & Gaud.) Th. & Rap.	216	21	++++
A. versicolor (Vuill.) Tiraboschi	226	21	++++
A. Sydowi (Bain. & Sart.) Th. & Ch.	247	21½	++++
A. terreus Thom	255	21½	++++
A. ustus (Bain.) Thom & Church	275	18½	++++
A. flavipes (Bain. & Sart.) Th. & Ch.	286	21	++++
A. candidus Link	308	21½	++++
A. alliaceus Thom & Church	315	21½	++++
A. niger v. Tieghem	319	22	++++
A. niger v. Tieghem	322	22	++++
A. niger v. Tieghem	334	22	++++
A. niger v. Tieghem	566	23½	++++
A. niger v. Tieghem	599	23½	++++
A. cinnamomeus Schiem.	348	21½	++++
A. carbonarius (Bain.) Thom	369	21½	++
A. Wentii Wehmer	377	22	++++
A. quercinus (Bain.) Thom & Church	387	22	++
A. ochraceus Wilhelm	398	22	++++
A. ostianus Wehmer	420	22	++++
A. terricola var. *americana* Marchal	424	22	++++
A. tamarii Kita	427	22	++++
A. luteo-virescens Blochwitz	444	22	++++
A. Oryzae (Ahlburg) Cohn	447	23	++++
A. flavus Link	482	23	+++
A. parasiticus Speare	502	23	++++
Penicillium Thomii Maire	701	22½	++++
P. javanicum v. Beyma	707	22½	++++
P. spinulosum Thom	723	22½	++++
P. roseo-maculatum Biourge	729	22½	++++
P. carmino-violaceum Dierckx	733	22½	++++
P. vinaceum Gilman & Abbott	739	22½	++
P. decumbens Thom	741	22½	++++
P. lividum Westling	754	22½	++++
P. implicatum Biourge	763	23½	++++
P. baiiolum Biourge	772	23½	++++
P. Waksmani Zal.	778	23½	++++
P. digitatum Sacc.	786	23½	++++

TABLE 2—(*Continued*)

Name	NRRL No	Age in months	Viability
P. oxalicum Currie & Thom	789	23½	++++
P. citrinum Thom	805	24	++++
P. chrysogenum Thom	807	24	++++
P. notatum Westling	824	24	++++
P. baculatum Westling	843	24	++++
P. Melinii Thom	847	23½	++++
P. puberulum Bainier	845	23½	++++
P. roqueforti Thom	849	23½	++++
P. stoloniferum Thom	859	23½	++++
P. ochraceum (Bainier) Thom	869	23½	++++
P. camemberti Thom	877	22½	++++
P. biforme Thom	886	21	++++
P. lilacinum Thom	895	21	++++
P. janthinellum Biourge	905	21	++++
P. nigricans Bainier	915	21	++++
P. terrestre Jensen	933	21	++++
P. cyclopium Westling	941	20	++++
P. viridicatum Westling	963	20	++++
P. expansum (Link) Thom	976	20	++++
P. italicum Wehmer	983	20	++++
P. Urticae Bainier	989	20	++++
P. patulum Bainier	994	20	++++
P. claviforme Bainier	1002	20	++++
P. duclauxi Delacr	1030	20	++++
P. islandicum Sopp	1037	20	++++
P. herquei Bainier & Sartory	1040	20	++++
P. rugulosum Thom	1045	20	++++
P. purpurogenum Stoll	1061	20½	++++
Gliocladium deliquescens Sopp	1086	20	++++
Glio. fimbriatum Gil & Abb.	1090	20	++++
Glio. roseum Bainier	1084	20	++++
Paecilomyces Varioti Bainier	1122	20	++++
Scopulariopsis brevicaulis (Sacc) Bain	1101	20	++++
Scop. brevicaulis var. *glabrum* Thom	1109	19	++++
Absidia coerulea (−) Bainier	1310	22	++++
Absidia coerulea (+) Bainier	1314	22	++++
Circinella spinosa (−) v. T. & le Mon.	1356	22	+++
Circinella spinosa (+) v T & le Mon.	1359	22	+++
Chaetocladium Brefeldii v T. & le Mon .	1349	22	+++
Coemansia pectinata Bainier	1564	19½	++
Cunninghamella echinulata (+) (Thax) Sacc.	1382	22	+++
Cunninghamella echinulata (−) (Thax) Sacc. .	1384	22	+++
Helicostylum sp. (+)	1396	21½	+++
Mucor genevensis Lendner	1412	21½	++++
Mucor hiemalis (−) Wehmer	1419	21½	++++
Mucor mucedo (+) Bref.	1424	21½	++++
Mucor mucedo (−) Bref.	1425	21½	++++
Mucor Rouxianus (Calmette) Wehmer	1429	22	++
Mycotypha microspora Fenner	684	21½	++++
Parasitella simplex (−) Bainier	1459	22	++++
Phycomyces Blakesleeanus (−) Burgeff	1464	21½	+++
Phycomyces Blakesleeanus (+) Burgeff	1465	21½	++
Rhizopus arrhizus Fischer. . . .	1470	21½	++++
Rhizopus nodosus Namysl. .	1474	21½	++++

TABLE 2—(*Continued*)

Name	NRRL No.	Age in months	Viability
Rhizopus nigricans (+) Ehrenberg	1477	21½	++++
Rhizopus nigricans (−) Ehrenberg	1478	21½	++++
Rhizopus nigricans (−) Ehrenberg	1483	21½	++++
Rhizopus nigricans (+) Ehrenberg	1484	21½	++++
Syncephalastrum sp. (−)	1485	21½	++++
Thamnidium elegans Link	1613	19½	+++
Zygorhynchus heterogamus (±) Vuill	1489	21½	+
Conidiobolus sp	1612	19½	−
Entomophthora apiculata Thaxter	1626	19½	−
Botryosporium sp	1710	19	++++
Botrytis sp	1285	19½	−
Botrytis spectabilis	1776	19½	++++
Cadophora Richardsiae Nannf	1630	19½	++++
Catenularia fuliginea Saito	1299	19	++++
Ceratostomella adiposum (Butler) Sart	1801	22	+++
Chaetomium globosum Kunze	1669	19	−
Cladosporium fulvum Cke	1671	19	++++
Dipodascus uninucleatus Biggs	1629	19½	+++
Epidermophyton interdigitale (Pr.) MacCar	1295	19	++++
Fusarium moniliforme Sheld	1675	19	+
Gymnoascus sp	1677	19	++
Helminthosporium sp	1680	19	++
Metarrhizium sp	1800	22	++++
Microascus trigonosporus Emm. & Dodge	1570	23½	+++
Monascus purpureus Went	1596	19½	+++
Monilia sitophila (Mont.) Sacc	1275	20½	++++
Sordaria fimicola (Rab.) Ces. & de Not	1558	19½	+
Stachybotrys lobulata Berk	1695	19	++++
Trichoderma Koningi Oud	1761	21	++++
Trichothecium roseum Link	1588	19½	+++
Tritirachium dependens Limber	1210	19	++++
Verticillium albo-atrum Rein. & Berth	1204	19½	++++

[a] ++++ = excellent viability
+++ = good viability
++ = fair viability
\+ = poor viability
− = no growth

spored member of the *A. niger* group; *A. quercinus* (NRRL *387*), a light-sporing, heavy sclerotium-producing member of the *A. ochraceus* group; and *A. ruber* (NRRL *55*), *A. niveo-glaucus* (NRRL *127*), and *A. echinulatus* (NRRL *131*), all ascosporic members of the *A. glaucus* group.

Low viability in *A. quercinus* probably resulted from the limited number of conidia contained in the dried suspension, and the limited growth of *A. carbonarius* may have been due at least in part to the large dimensions of its conidia. Three of the five

strains showing limited viability belonged to the *A. glaucus* group, and two of these, *A. niveo-glaucus* and *A. echinulatus*, possessed large conidia and ascospores, suggesting the possibility that large-spored members of this group may not lend themselves well to preservation by the lyophil method. Small-spored species of the same group such as *A. Chevalieri*, *A. repens*, and *A. Amstelodami*, on the other hand, consistently showed excellent viability and growth. *A. niger*, NRRL *599*, which had shown poor viability in the tests of selected cultures reported above, showed excellent viability in the present series. Among five strains of *A. niger* included for the purpose of comparing different representatives of a single species, no apparent difference in viability was observed.

Penicillium and allied genera: Altogether 40 strains of *Penicillia* representing a like number of species were tested. Included were representatives of such well-known and widely discussed species as *P. notatum*, *P. chrysogenum*, *P. patulum*, *P. claviforme*, and *P. roqueforti*. Excellent viability was obtained from lyophil preparations of all species with the exception of *P. vinaceum*, in which growth was only fair (TABLE 2); as in the earlier tests (TABLE 1), limited growth is believed to have resulted more from a dearth of conidia in the lyophil preparation than from any marked inability of the culture to withstand the freezing-drying process. Subsequent microscopic examination of a duplicate lyophil preparation revealed the presence of comparatively few spores.

Lyophil preparations of six representative forms belonging to the related genera *Gliocladium*, *Scopulariopsis*, and *Paecilomyces* showed excellent viability and growth (TABLE 2).

In all cases, colonies developing from lyophil preparations appeared typical of the strains under observation. Microscopic examination provided confirmatory evidence.

Mucorales: Viability tests were made on 27 strains of the Mucorales representing 19 different species. Of this number, plus and minus strains were included for 6 species, and for the single species, *Rhizopus nigricans*, 2 plus and 2 minus strains were tested. Results are presented in table 2. Excellent or good growth was obtained in all cases with the exception of *Mucor Rouxianus*, NRRL *1429*, a strain of *Phycomyces Blakesleeanus* (+), NRRL *1465*, *Coemansia pectinata*, NRRL *1564*, and *Zygor-*

hynchus heterogamus, NRRL *1489.* In the last of these cultures viability and growth were poor, and examination of a second lyophil preparation from the original set of 4 revealed the presence of numerous zygospores but very few sporangiospores. Microscopic examination of duplicate preparations of *Phycomyces* and *Coemansia* revealed the presence of comparatively few spores.

Cultures developing from lyophil preparations of all of the Mucorales appeared typical.

Entomophthorales: Representatives of the Entomophthorales that were tested for viability have shown consistently negative results. Included in the present survey were strains of *Entomophthora apiculata,* NRRL *1626,* and *Conidiobolus* sp., NRRL *1612.* A second strain of *Conidiobolus,* NRRL *1255,* has been subsequently investigated. For each of these cultures a new series of lyophil preparations has been made, and viability tests have been conducted within a few days. In no case has growth been obtained. The method as employed by us is obviously not applicable to this group.

Miscellaneous genera: Viability tests were conducted on 23 cultures representing an equal number of genera, belonging mostly in the Fungi Imperfecti. Results are shown in table 2. Excellent to good viability was obtained in most cases, but negative results were obtained with *Chaetomium globosum,* NRRL *1669,* and *Botrytis* sp., NRRL *1285.* The first of two preparations of *Sordaria fimicola,* NRRL *1558,* was negative, whereas a duplicate tube yielded very few colonies. Duplicate lyophil preparations of each of the above-named cultures were subsequently examined microscopically; numerous hyphal fragments were observed, but no spores were found. This absence of spores possibly accounts for the inconsistent growth of *Sordaria* and for the lack of growth in *Chaetomium* and *Botrytis.* Such an explanation derives additional support from tests subsequently performed in which new lyophil preparations, containing ample spores, were made of these strains and were tested for viability. Results were positive. It should, of course, be borne in mind that in the latter tests no time element was involved, whereas the preparations found negative were already 19 months old.

Poor viability characterized a preparation of *Fusarium moniliforme*, NRRL *1675*, although a duplicate tube was found to contain abundant spores—no explanation is available. In recent tests, preparations of *Fusarium bulbigenum* var. *Lycopersici*, NRRL *1985*, have shown excellent viability when tested immediately after being processed.

PRESERVATION OF PENICILLIN-PRODUCING CULTURES

In the investigation of any fermentation, the importance of maintaining cultures in a stable and highly productive state cannot be overemphasized. In the production of penicillin, the problem of culture preservation assumes special significance because of the marked tendency for highly productive strains to vary, or mutate, when frequently transferred, or when grown upon nutrient-rich substrata (Raper and Alexander, **1945**). The need for a simple and satisfactory method of maintaining stock cultures was recognized early in the work on penicillin. Since the autumn of 1941, multiple lyophil preparations (often running up to 30 to 60 tubes) have been made of cultures which seemed to offer particular promise.

As our investigations have progressed, it has frequently been desirable to compare penicillin production by strains in current use with those employed in earlier experiments. In a number of cases, such comparisons have been made between fresh stock cultures and cultures of the same strains from lyophil preparations of varying age up to 40 months. In making these comparisons, the culture medium and methods reported by Raper, Alexander, and Coghill (**1944**) were employed. Results obtained with several series of such cultures are presented in table 3. Paired entries represent parallel cultures of the same strain, derived in the one case from the recultivation of a lyophil preparation, in the other case by transfer from the stock culture. The term "stock culture,"[7] refers to agar slant cultures maintained in duplicate in

[7] In the case of the *Penicillia*, such stock cultures are regularly transplanted on Czapek's solution agar, allowed to grow at room temperature for a period of 2 to 3 weeks, and then stored in a refrigerator at 3° to 5° C. for a period up to 8 months, during which time no further growth occurs, and the cultures remain in a dormant state.

our permanent collection under conditions believed to be optimum for preserving the mold in a stable and viable form. Subcultures seeded from current stocks of various strains of *P. notatum* and *P. chrysogenum* are employed in our work, and, when transplanted upon sporulation media (Moyer and Coghill, **1945**), grow rapidly and produce a heavy and uniform sporulation. At the same time, it has been our consistent experience that lyophilized cultures of these same strains planted upon similar media produced uniform and abundant crops of spores equal in all respects to plates seeded from the agar stock cultures. This being true, it has been possible to inoculate surface production flasks with equal and like quantities of spores developed from these two different sources.

Similarities or differences in yields of penicillin, pH, and dry weights of the mycelia can be interpreted as resulting from similarities or differences existing between the strains maintained by these different methods of preservation, since in any pair of cultures the substrate was of exactly the same composition, the temperature of incubation was constant, and inoculations were as nearly uniform as it was possible to make them.

Examination of the results presented in table 3 clearly indicates that cultures of *P. notatum* and *P. chrysogenum* can be preserved by the lyophil technique for periods up to 3 years without loss of their capacity to produce penicillin. In general, penicillin yields and pH values agreed quite closely in the parallel cultures from day to day; and in 9 of 13 cases, the cultures seeded from the lyophil source actually showed slightly higher average yields of penicillin than those seeded from stock cultures grown upon agar. This difference, however, is not marked, and it is probably not significant. In every case investigated, the mycelial mats developed from lyophil "seed" and those from stock "seed" appeared strikingly similar. In the majority of cases, this cultural similarity was likewise reflected in the approximately equal weights of the dried mycelial mats harvested from individual flasks (TABLE 3).

While comparative data need not be presented, it should be noted that selected strains maintained in lyophil form have retained unaltered their capacity to produce penicillin in submerged culture.

TABLE 3

PENICILLIN PRODUCTION IN SURFACE CULTURE BY SELECTED STRAINS OF PENICILLIUM NOTATUM WESTLING & P. CHRYSOGENUM THOM (1) PRESERVED IN LYOPHIL FORM AND (2) MAINTAINED UPON CZAPEK'S SOLUTION AGAR SLANTS UNDER OPTIMUM CONDITIONS

Name	NRRL no.	Type of culture	Age in mos.	Penicillin production: Penicillin yields, 4th Day		5th Day		6th Day		7th Day		Mat weights in grams: Flasks		
				pH	units[a]	pH	units	pH	units	pH	units	A	B	C
P. chrysogenum	807[b]	Lyo.	24	7.0	29	7.6	53	7.9	59	8.0	53	.926	.931	.982
P. chrysogenum	807	Stock[c]		6.9	25	7.5	45	7.9	56	7.8	50	1.004	.953	.942
P. chrysogenum	811	Lyo.	32	6.5	25	7.3	50	7.8	67	8.0	63	1.010	1.033	1.071
P. chrysogenum	811	Stock		6.3	25	7.1	45	7.6	60	8.0	59	.956	.979	1.018
P. chrysogenum	811	Lyo.	40	7.3	44	7.6	78	7.9	85	8.3	76	.911	.909	1.053
P. chrysogenum	811	Stock		7.1	43	7.4	73	7.8	83	8.3	90	.914	.943	1.027
P. notatum	824[d]	Lyo.	22	7.6	78	7.8	88	8.1	80	8.3	58	.941	.958	.964
P. notatum	824	Stock		7.4	78	8.0	82	8.1	74	8.3	62	.945	.949	.965
P. notatum	824	Lyo.	32	7.3	78	7.6	98	7.9	92	8.2	79	.843	.855	.877
P. notatum	824	Stock		7.5	78	7.8	90	8.1	81	8.4	40	.705	.663	.718
P. notatum	832[e]	Lyo.	24	7.6	53	7.9	70	8.1	52	8.4	26	.920	.929	.957
P. notatum	832	Stock		7.5	45	7.9	64	8.1	56	8.4	32	.869	.946	.941

[a] Yields of penicillin are expressed in Oxford units per milliliter.
[b] Type strain of *P. chrysogenum* Thom (Thom's No. 26).
[c] The "stock" cultures employed were current stocks, maintained on agar, from the permanent mold collection. They varied in age from 2 or 3 weeks to 5 or 6 months.
[d] The unimproved Fleming strain.
[e] Strain commonly employed for the production of penicillin in submerged culture.

TABLE 3—(*Continued*)

Name	NRRL no.	Type of culture	Age in mos.	Penicillin production: Penicillin yields								Mat weights in grams		
				4th Day		5th Day		6th Day		7th Day		Flasks		
				pH	units[a]	pH	units	pH	units	pH	units	A	B	C
P. notatum	1209[f]	Lyo.	25	7.6	75	7.9	85	8.0	68	8.3	43	.921	.935	.937
P. notatum	1209	Stock		7.3	75	7.6	65	8.1	68	8.3	45	.952	1.172	.968
P. notatum	1209	Lyo.	35	7.6	76	7.8	92	8.1	88	8.3	68	.823	.771	.970
P. notatum	1209	Stock		7.5	78	7.8	100	8.1	106	8.3	73	.759	.745	.813
P. notatum	1248	Lyo.	20	7.4	80	7.9	72	8.0	76	8.4	43	.970	.974	.971
P. notatum	1248	Stock		7.5	85	7.9	90	8.1	72	8.4	39	.980	.953	.962
P. notatum	1249	Lyo.	19	7.0	91	7.8	103	7.8	82	8.2	60	.776	.797	.807
P. notatum	1249	Stock		7.1	98	7.6	103	7.8	82	8.1	74	.792	.784	.801
P. notatum	1249	Lyo.	32	7.3	92	7.5	120	7.9	114	8.2	103	.758	.747	.847
P. notatum	1249	Stock		7.3	76	7.6	88	7.9	90	8.2	96	.905	.893	.937
P. notatum	1249.B21[g]	Lyo.	11	6.8	90	7.5	125	8.0	130	8.3	72	.766	.782	.844
P. notatum	1249.B21	Stock		7.0	92	7.7	115	8.1	111	8.3	63	.835	.851	.901
P. notatum	1249.B21	Lyo.	20	6.8	101	7.3	150	7.7	162	8.1	162	.787	.746	.831
P. notatum	1249.B21	Stock		6.8	98	7.2	137	7.7	159	8.1	148	.793	.788	.863

[f] Fleming strain as investigated by Drs. Florey, Heatley et al. in 1940–1941.
[g] Strain generally used for the production of penicillin in surface culture. Descended from the Fleming isolate; an improved strain developed at the Northern Regional Research Laboratory.

In some cases, as many as 60 replicate lyophil preparations have been prepared from a single good penicillin-producing culture, and during the ensuing months individual tubes have been opened from time to time to furnish inoculum comparable to that used in earlier experiments. In no case have we observed any decrease in the apparent viability of such cultures, as progressively older tubes have been opened, nor have we detected any reduction in their capacity to produce penicillin, although some of these are now more than 2½ years old. Lyophil preparations of *P. notatum*, NRRL *1249.B21* (the strain generally employed in industry for the surface production of penicillin), in particular, have been opened and tested frequently since this strain was first isolated. Where these preparations have been employed, penicillin yields have varied from experiment to experiment, just as they do when flasks are seeded from agar stock cultures, but no consistent change has been observed. It is our belief, therefore, that the lyophil technique provides an excellent means of preserving selected penicillin-producing cultures in unaltered form over long periods.

DISCUSSION

Although tests have not been in progress long enough to evaluate thoroughly the lyophil technique as a means of extending the viability of molds, much evidence is accumulating which indicates that this objective will, in all probability, be realized. Many strains have now been maintained in desiccated form for approximately 3½ years. In most cases there has been no apparent decrease in viability in the successively older preparations that have been examined, and in no instance has there been a marked decrease in viability with increased time. Furthermore, all cultures grown from lyophil preparations have appeared wholly typical of the strains under observation in both colony characteristics and in structural details.

The present investigations have been conducted on an extensive scale, and it now appears probable that most of the molds producing comparatively small aerial spores, or conidia, can be successfully preserved by the lyophil method. Excellent results have been obtained, almost without exception, with the *Penicillia* and closely allied forms. Most of the *Aspergilli* have been processed quite

satisfactorily, although the large-spored, ascosporic species of the *Aspergillus glaucus* group did not lend themselves well to this technique. Species of the Mucorales which produced abundant sporangiospores have been preserved satisfactorily, and tests completed up to the present time indicate that the period of viability of many members of this group is substantially extended by preservation in lyophil form. Consistently negative results have been obtained with the limited number of the Entomophthorales investigated. Positive, and, in most cases, satisfactory results were obtained with the Fungi Imperfecti. Strains of *Sordaria* and *Chaetomium*, which yielded negative results in initial tests, proved positive when new preparations containing abundant spores were made.

No attempts have been made to preserve any of the Myxogastrales or of the aquatic Phycomycetes. Spores of the Acrasiales, or pseudoplasmodium-forming slime molds, have been preserved with excellent results for periods up to 41 months, when last tested. Attempts to preserve the myxamoebae, or vegetative cells, of these same forms have been unsuccessful.

While many of the variations involved in the processing of large numbers of cultures have not been thoroughly investigated, certain general observations have been made which are believed significant. Cultures producing small spores in abundance have been preserved most satisfactorily. Cultures producing large spores have been preserved less successfully. Cultures producing large, highly organized spores, such as the primary conidia of *Conidiobolus* and *Entomophthora*, have failed to withstand the freezing-drying process. Preparations containing very few spores often yielded positive results, but preparations containing only vegetative mycelium in the form of hyphal fragments, and no specialized propagative bodies, regularly yielded negative results. It would appear that the presence of spores, conidia, or other definite propagative cells is essential for satisfactory lyophilization. Such cells should be present in abundance and the smaller their dimensions, the greater the probability that the species can be successfully preserved in desiccated form.

Not only do cultures preserved in lyophil form retain their distinctive cultural and morphological characteristics, but in all cases where tests have been made, physiological characteristics have like-

wise remained stable. Two examples will be cited. Cultures of penicillin-producing molds maintained in lyophil form for periods up to 40 months produce yields of penicillin equal to the same strains maintained in agar slant cultures under optimum conditions. In fact, lyophilized cultures have in many cases yielded slightly higher values than agar cultures, but it is doubtful whether the observed differences are significant. Itaconic acid-producing strains of *Aspergillus terreus* maintained in lyophil form for 40 months, when recultivated and tested, produced yields of itaconic acid [8] almost identical with those produced by cultures of the same strains recultivated four times and maintained for the same period on agar slants under optimum conditions. Brown (**1932**), Swift (**1937**), Elser, Thomas and Steffen (**1935**), Osterman and Rettger (**1941**), and others reported that bacteria so preserved retained their toxigenic and serological characteristics.

It is believed that the greatest usefulness of the lyophil technique as a means of preserving molds probably lies in the field of industrial fermentations. Using this method it is possible to make an unlimited number of dried preparations from a single and uniform suspension of spores taken from a selected culture or actual fermentation. Subsequent to this, one of these dried cultures can be opened and its contents recultivated whenever necessary with the assurance that the new growth will result from the spores originally processed. It is thus possible to set fermentations over an extended period with inoculum developed from an entirely uniform source. The possibility of contamination during storage is eliminated since the cultures are sealed in glass. It has been fully established in our studies that lyophilized cultures of *P. notatum*, NRRL *1249.B21*, and other high-yielding strains, retain at a high and stable level their capacity to produce penicillin. Replicate cultures from a single set of preparations have been opened from time to time over a period of almost 2 years, and uniformly satisfactory yields have been obtained. In fact, it is now our regular practice to check current stock cultures against such lyophilized preparations whenever any question arises regarding possible diminution in penicillin-producing capacity.

[8] The writers are indebted to Dr. L. B. Lockwood for making these comparisons.

SUMMARY

1. Almost all of the *Aspergilli* and *Penicillia* can be preserved in lyophil, or desiccated form. Such evacuated preparations, tested at intervals up to 40 months, generally showed no reduction in viability, and resulting cultures were entirely typical of the strains under observation.

2. Representative species of the Mucorales have been successfully preserved, and in the case of *Rhizopus*, *Phycomyces*, and other genera there is evidence of a marked extension of viability.

3. Attempts to preserve members of the Entomophthorales have been unsuccessful.

4. Representative Hyphomycetes were viable when tested at approximately 20 months.

5. Molds preserved in lyophil form apparently retain their biochemical and physiological characteristics in unaltered form. Strains of *Aspergillus terreus* preserved in this manner produced undiminished yields of itaconic acid after 40 months, while strains of *P. notatum* and *P. chrysogenum* retained at original levels their capacity to produce penicillin.

6. The lyophil technique provides a convenient means of preserving a large number of replicate cultures which can be used as seed material for standard cultures or to set series of fermentations over an extended period of time. Storage becomes a minor problem because of the small dimensions of the preparations. The possibility of contamination is eliminated during the storage period.

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THE CLASSIFICATION OF THE TREMELLALES

G. W. MARTIN

(WITH 1 FIGURE)

I

The classification of the Tremellales cannot be considered without reference to that of the Basidiomycetes as a whole, since the limits of the order, its presumed relationships with other orders and the interrelationships between its subdivisions are all parts of the larger problem. It seems desirable, therefore, to review briefly the varying concepts of the Basidiomycetes which have found more or less acceptance during the past two generations.

The treatment of the fungi in the earlier editions of Sachs's *Lehrbuch* (27) may be regarded as representing the viewpoint widely held at the beginning of the modern period. Sachs divided the fungi into four major groups, the Phycomycetes, the Hypodermiae (rusts and smuts), the Basidiomycetes and the Ascomycetes. In Goebel's adaptation of the Sachs text (18) the major groups were increased to six by the addition of the Chytridieae and the separation of the smuts and rusts, the former relegated to a place between the chytrids and the Phycomycetes; the latter put between the Ascomycetes and the Basidiomycetes. In both, the lichens are included in the Ascomycetes and the Myxomycetes are set apart from the other groups.

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In 1884, the German edition of de Bary's great work (1) appeared. De Bary, like Goebel, made the Uredineae a class coordinate with the Ascomycetes and Basidiomycetes and inserted between them. He placed the Ustilagineae with and after *Protomyces,* before the Ascomycetes, noting that he did not believe the smuts to be closely related to the rusts. He divided the Basidiomycetes into the Hymenomycetes and Gastromycetes. In connection with the former he stated: "In the simplest cases, such as . . . *Corticium, Dacryomyces, Exobasidium* and some species of *Hypochnus,* the compound sporophores do not vary essentially in form and differentiation from the layers of teleutospores in the Uredineae . . ." (1, p. 287). He regarded each cell of the divided basidia of *Auricularia* and *Exidia* as a separate basidium bearing a single spore.

De-Toni (13), in the first treatment of the smuts and rusts in the *Sylloge Fungorum,* referred to the asci in both groups. C. E. Bessey (2, p. 340) at first classed them with the Ascomycetes, but later (3) erected for them the class Teliosporae, coördinate with the Ascosporae and Basidiosporae. In this he was followed by Clements and Shear (8) and E. A. Bessey (4). The majority of other students writing since the beginning of the present century have recognized the smuts and rusts as Basidiomycetes. An obsolete terminology has persisted, however, which applies distinct names to structures in these fungi which appear to be entirely homologous with those designated by other terms in other Basidiomycetes, and this may have had more weight than is commonly realized in influencing their separation from certain of the Tremellales.

The classification of the Basidiomycetes which is most familiar at the present time reflects very largely the conclusions of Brefeld. In the first summary of his results, Brefeld (6, pp. 270–274) derived the smuts from the conidial Zygomycetes but did not include them in the Basidiomycetes, which he envisaged as having had an independent origin from the same source. The Basidiomycetes were divided into the Protobasidiomycetes, with septate basidia (Uredineen, Auricularieen, Tremellineen, Pilacreen), and the Autobasidiomycetes, with non-septate basidia. The Dacrymycetaceae and the Tulasnellaceae were included in this second

subclass with the thelephores, agarics and puffballs. In a subsequent volume (**7**, pp. 341–356), Brefeld recognized the smuts as a distinct class, the Hemibasidii, coördinate with the Ascomycetes and Basidiomycetes, and suggested that the Protobasidiomycetes had arisen from the Ustilaginaceae and the Autobasidiomycetes from the Tilletiaceae. Even while the later volumes of the *Untersuchungen* were appearing, cytological evidence was beginning to accumulate which was destined to destroy the foundations of the edifice which Brefeld had erected. Nevertheless, his system was adopted, with some modification, notably the unequivocal inclusion of the smuts in the Basidiomycetes as the class Hemibasidii, but with explicit adoption of his theory of the origin of basidia from conidiophores, by Lindau and Dietel in the first edition of Engler and Prantl. The wide popularity and extreme usefulness of that work quite naturally resulted in the acceptance of its classification by nearly all the textbooks and most of the systematic treatments published during the next third of a century. It remains the dominant treatment to-day.

An alternative classification, first outlined by Patouillard in 1887 (**23**) and greatly elaborated in his *Essai Taxonomique* of 1900 (**24**), proposed the division of the Basidiomycetes into two subclasses, the Hétérobasidiés, characterized by basidiospores which, in germination, habitually produce secondary spores and with basidia septate or deeply divided, and the Homobasidiés, bearing basidiospores which consistently germinate by the production of a mycelium and with cylindrical or clavate, undivided basidia. In the Hétérobasidiés, Patouillard recognized four families: the Auriculariaceae, with transversely septate basidia, in which he included the rusts and smuts, the Tremellaceae, with cruciate-septate basidia, the Tulasnellaceae and the Caloceraceae (*i.e.*, Dacrymycetaceae).

One great merit of Patouillard's arrangement is that instead of insisting upon rigid adherence to a single arbitrarily selected character he made his scheme elastic enough to permit the insertion of groups where they fit naturally on the basis of all characters taken together, as illustrated by his inclusion of the Tulasnellaceae and the Dacrymycetaceae in the Heterobasidiomycetes. Patouillard's own subsequent investigations did much to fortify his system, but

it was not until its adoption by Bourdot and Galzin in their notable series of papers on the Hymenomycetes that much attention was paid to it outside of France. The treatment of Coker (**9**) was in general accord with it, while its use by Rea in the British Basidiomycetes (**25**) and the publication of Bourdot and Galzin's great volume (**5**) compelled the mycological world to grant it respectful consideration.

Gäumann (**16**) divided the Basidiomycetes into Protobasidiomycetes, with the four orders Auriculariales, Uredinales, Ustilaginales and Tremellales, and Autobasidiomycetes, including the Tulasnellales and the Dacrymycetales in the latter groups. This is clearly based on Brefeld's system, somewhat modified and with emphasis on the chiasto-stichobasidial concepts of Maire and Juel. In Gäumann and Dodge (**17**) the treatment of the Basidiomycetes is radically altered. Starting with the Polyporales, in which are included, among others, the Tulasnellaceae and two rather dubious associated families, they follow them with the Agaricales, Cantharellales, Gasteromycetes, Dacrymycetales, Auriculariales, Uredinales and Ustilaginales, in the order named. Their treatment is admittedly influenced by the chiasto-stichobasidial theory so striking a feature of Gäumann's book, but in a foot-note (p. 413) Dodge recognizes that this has been overstressed.

In the second edition of Engler and Prantl (**6**: vii. 1928) the Basidiomycetes are divided into the subclasses Hemibasidii and Eubasidii. The Hemibasidii, by Dietel, includes the orders Ustilaginales and Uredinales, the two smut families separated as suborders, with reaffirmation of Brefeld's theory of the origin of basidia from conidiophores. The Eubasidii embraces the single order Hymenomycetae, with the Tremellineae, Hymenomycetineae and five Gasteromycete groups as suborders. In the special treatment of the Gasteromycetes by E. Fischer (**15**), however, the Gasteromycetes are ranked as an order, with six suborders. In his treatment of the Tremellineae, Killermann (**20**) recognizes three families, the Auriculariaceae, with the tribes Auricularieae and Phleogeneae, the Tremellaceae, with the tribes Sirobasidieae, Tremelleae and Hyalorieae, and the Dacrymycetaceae. In its recognition of the affinity of the Dacrymycetaceae with the groups possessing septate basidia, this is a definite advance over Brefeld's

classification. *Tulasnella* is included in the Tremelleae, where it could never be located by following the keys. Gwynne-Vaughan and Barnes (**19**) follow what is essentially Brefeld's system, including *Tulasnella* in the Thelephoraceae and merging the Dacrymycetaceae in the Clavariaceae. Bessey (**4**) adopts the name Heterobasidieae to include the orders Auriculariales, Tremellales and Dacrymycetales, excluding *Tulasnella,* with reservations, to the Thelephoraceae. Smith (**28**) divides the Basidiomycetes into the Eubasidii, with the orders Agaricales, Lycoperdales (including all Gasteromycetes), Dacrymycetales, Tremellales and Auriculariales, and the Hemibasidii, embracing the rusts and smuts.

It is evident that there is no general agreement either as to the basic division of the Basidiomycetes or as to the relative rank and limits of the various subdivisions. On the whole, the tendency in recent years has been to group the Dacrymycetaceae with the tremellaceous fungi and to recognize three orders of these fungi, based on the cruciate-septate, transversely septate and forked types of basidia. There has also been a tendency to emphasize the separation of the Auriculariaceae from the rusts by including these groups in different major subdivisions of the Basidiomycetes.

As has been stressed by Linder (**21**), the inadequate fossil record of the fungi compels us to base our ideas of their phylogeny upon evidence derived from the comparative study of living species, all of which have had abundant time in which to acquire modifications, and it is not easy to determine which characteristics resemble those of the hypothetical ancestral forms and which are of more recent origin. In the case of the lower Basidiomycetes, we have a more than usually complete series of transitional forms, constituting a network which may be traversed in almost any direction and in which, as in the peccary and tapir trails of a tropical forest, it is amazingly easy to become lost unless, before entering, one is careful to establish distinctive landmarks.

For the purposes of the present discussion, I shall adopt, as points of reference, the following postulates:

1. The fundamental character in the Basidiomycetes is the nature of the basidium, to which all other characters are subordinate.

2. It is to be expected that in all categories basic groups will, in general, be characterized by greater morphological simplicity and

flexibility than the more specialized and presumably derivative groups.

3. In derivative saprobic groups, the basidium tends to become stabilized and, in such groups, the organization of the basidiocarp becomes increasingly significant.

4. Adaptation to parasitic nutrition is an indication of relative specialization as compared with saprobism. It follows that parasitic forms may readily be conceived to have arisen from saprobic forms but that the reverse process is more difficult to explain.

With these as a guide, I shall attempt to defend the following theses:

I. That the primary division of the Basidiomycetes into Heterobasidiomycetes and Homobasidiomycetes, as proposed by Patouillard, furnishes the best basis for a natural system which has thus far been suggested.

II. That within the Heterobasidiomycetes, three, or at most four orders should be recognized: the Tremellales, Uredinales, Ustilaginales and possibly the Septobasidiales, and that within the Tremellales, in the inclusive sense, the transitions between the various types of basidia are such as to make untenable the maintenance of the Auriculariales and Dacrymycetales as distinct orders.

III. That the Tremellales, more than either the Uredinales or Ustilaginales, retains the largest number of primitive characters and that within its limits, as here defined, there exist forms which afford a satisfactory transition to the rusts, on the one hand, and to the Homobasidiomycetes, on the other.

All modern systems which separate the smuts, as Hemibasidiomycetes, from all other Basidiomycetes are, as stated, based on Brefeld's theory of the origin of basidia from conidiophores. No additional reasons have been advanced for this disposition of the group and with the collapse of the theory on which it was based the only reasons for continuing to employ it are inertia and adherence to tradition.

The systems which place the rusts and smuts together but separate them from the rest of the Basidiomycetes are more defensible, since there is much reason to suppose that these two orders may be closely related, but they are defective in their failure to give

adequate recognition to the many similarities between the rusts and certain of the auriculariaceous genera. Even if, as Linder and others suppose, the rusts constitute the basic basidiomycete order from which other Basidiomycetes have been derived, this criticism is still valid.

The systems which include the rusts and smuts together with those tremellaceous fungi with cruciate-septate or transversely septate basidia in a single series, but relegate the Dacrymycetaceae and Tulasnellaceae to another series as homobasidiate fungi, are, in the case of the Dacrymycetaceae, stressing a single character to the exclusion of numerous others which point to the heterobasidial nature of the family, and, in the case of the Tulasnellaceae, substituting a far-fetched and wildly improbable theory of the nature of the tulasnellaceous basidium for a simple and obvious one.

As compared with these schemes, and on the basis of known living representatives, the concept of the Heterobasidiomycetes and Homobasidiomycetes as representing two parallel series, very close together—scarcely separable in fact—at the hypothetical bases, but each developing in its own distinctive fashion quite independently of the other, fits the known facts far more accurately.

II

For the purposes of the present discussion, it may be assumed that the great majority of mycologists are content to recognize the adequacy of according ordinal rank to the Uredinales and Ustilaginales. But, as has been noted, there has been great difference of opinion as to the arrangement and rank of the remaining groups. To support the thesis that they may all be included in a single order, it is necessary only to demonstrate that the different types of basidia are more variable and that the intergradations between these types are more frequent than has commonly been supposed. Without, at this time, considering any phyletic implications, it may be profitable to start with *Ceratobasidium*, certainly a genus in which most of the few known species are among the morphologically simplest of the Basidiomycetes. The loose weft of hyphae which suggests rather than constitutes a basidiocarp; the short, thick basidia with their swollen epibasidia, borne in waxy tufts; the germination of the basidiospores by repetition—all combine to

create a strong suggestion of primitiveness. As noted by Linder, the resemblance of *Ceratobasidium* to the species of *Pellicularia* (*Botryobasidium*) makes it possible to connect the genus with the whole series of Homobasidiomycetes. On the other hand, aside from the fact that the epibasidia are not cut off from the hypobasidium by septa, they are in every respect so like the Tulasnellas that in a recent treatment (22) I have felt justified in including them in the Tulasnellaceae. Again, in *Ceratobasidium sterigmaticum* we have so close an approach to the Dacrymycetaceae, as represented by *Ceracea crustulina,* that placing the two species in distinct families can be justified only on the ground that, despite the recognized similarities at this level, the Dacrymycetaceae does constitute, on the whole, a compact and homogeneous group of genera representing one line of development, not, however, to be separated by more than a family line from other groups which can be connected with the same center.

The differences between the *Tulasnella* basidium and the cruciate-septate type, while very real, should not be over-emphasized. In the tenuous and more arid Sebacinas the basidia may be as widely scattered as in any *Tulasnella* or *Ceratobasidium*, and in some of these the epibasidia may be entirely lacking, each segment of the mature basidium giving rise directly to a sterigma and a spore. In such basidia there may be a marked tendency for the basidial cells to separate at maturity. But in most cases the epibasidia are well developed and in the soft and highly gelatinized large Tremellas, represented by *T. mesenterica,* they are enormously thickened at the apex, terminating in a bulbous tip which supports a sharply differentiated sterigma. When to this is added the presence of an empty, basal stalk-cell, cut off in basidial development, and the strongly lobed and often nearly separate divisions characteristic of *Protohydnum* and certain species of *Sebacina,* the resemblance to *Tulasnella* is not entirely fanciful.

Irregularities in number and orientation of septa are common in many tremellaceous fungi with cruciate-septate basidia and these sometimes approach remarkably closely to the transversely septate type. We are not, however, dependent upon these abnormalities to make the transition to the Auriculariaceae. In the genus *Patouillardina* the probasidia are elongate-fusiform, the primary

septum is regularly transversely oblique and the secondary septa are at right angles to it, usually reaching it, but not infrequently extending to the basidial wall, each cell so formed sending out a tortuous epibasidium to the surface of the waxy-gelatinous hymenium, and the whole structure, except for the orientation of the septa, remarkably like a *Platygloea* or an *Auricularia* basidium.

In *Auricularia* the probasidium as a whole is divided by transverse septa into four equal portions, fundamentally as in *Patouillardina,* each portion sending out a single tortuous epibasidium to the surface, where again definitive sterigmata are produced. Through *Platygloea* there is transition to *Helicogloea,* with its peculiar saccate probasidium, and, presumably independently, to the as yet unnamed species of *Herpobasidium* on *Lonicera* and to *Eocronartium, Jola* and *Cystobasidium,* all with definite and, in the last-named genus, somewhat thick-walled probasidia, strongly suggestive of the teliospores of rusts. Significantly associated with this resemblance is the parasitic habit characteristic of the species belonging to these genera.

The *Phleogena* basidium and spores have little in common with those of the other transversely septate groups and the associated genera in the Phleogenaceae are too little known to justify much speculation as to relationships with other groups, but it would not be surprising if further study of *Pilacrella* and similar genera were to indicate that *Phleogena* represents the terminus of its own developmental line.

Septobasidium deserves very special consideration. The curious symbiotic-parasitic relation with scale insects, almost exactly paralleling that of the lichen fungi with their host algae and resulting in a suggestively similar thallus, has led Couch (11), to whose researches we are indebted for the great bulk of our knowledge of the genus, to claim for it ordinal rank. Opposed to this conclusion, however, is the almost complete gradation of the probasidia from those in which they are scarcely more specialized than in *Auricularia,* through forms with a thin-walled but persistent hypobasidium to those in which the probasidium closely resembles a rust teliospore and functions like one. The relationship of the genus with the rusts is further emphasized by the existence of *S. Polypodii* Couch, which was later assigned to the rusts by

its author, principally because it does not parasitize scale insects, and the curious genus *Uredinella* Couch (**10, 12**), distinctly intermediate between the two groups.

The small families Sirobasidiaceae and Hyaloriaceae need not be discussed at length. The catenulate basidia of *Sirobasidium* are not rarely matched in *Gloeotulasnella pinicola* and may occasionally be observed in several species of *Tulasnella.* The lack of epibasidia and sterigmata is more significant. It may be that the spores are really homologous with epibasidia or perhaps the suppression of sterigmata represents a response on the part of immersed basidia analogous to that which has resulted in the sessile spores of certain Gasteromycetes. The latter comment might be applied in a slightly different sense to *Hyaloria,* in which the basidiospores are borne on slender stalks which are neither epibasidia nor functional sterigmata, but more like the stilt-like structures found in the Lycoperdaceae, and, like them, display a tendency to break some distance below the spores. Aside from this peculiarity, there is little to separate *Hyaloria* from the Tremellaceae. In any event, no one has seriously suggested that either of these families deserves elevation to the rank of an order.

III

I have already suggested that morphological simplicity, flexibility of expression of characters and a saprobic habit may be interpreted as indicating primitive position among these fungi as contrasted with morphological complexity, relative stability of characters and a parasitic habit. To these might be added germination by repetition as contrasted with germination by a mycelial tube, despite the fact that it is widespread among the Heterobasidiomycetes as a whole. It is, of course, recognized that an organism may be primitive in some respects and advanced in others.

The lack of a highly developed basidiocarp in the Heterobasidiomycetes as compared with the Homobasidiomycetes and the slight economic importance of the mainly saprobic Tremellales as compared with that of the rusts and smuts are doubtless largely responsible for the fact that the classification of the Tremellales has lagged so far behind that of the groups named. Most of the species of Tremellales are resupinate and the most elaborately or-

ganized *Tremella* or *Dacryomitra, Phlogiotis* or *Phleogena* is no more complicated than a *Stereum* or a *Clavaria* and far below the organizational level of the hemiangiocarpous boletes or agarics, to say nothing of the phalloids and most of the other Gasteromycetes. On the other hand, the basidia in the Heterobasidiomycetes as a whole as in individual species of the group are much more variable than in the Homobasidiomycetes.

Linder regards the pustulate fructification as more primitive than the resupinate and cites this as evidence of the basic character of the rusts. But a pustulate origin of resupinates is extremely common and is well illustrated by species of *Tulasnella, Arrhytidia* and *Sebacina*. In *Stypella* and in several of the minute species of *Tremella* the fully mature basidiocarps remain pustulate. The distinction seems to be of subordinate importance.

The basidia of certain of the Heterobasidiomycetes are notoriously variable both in number of spores produced and in septation. Coker (9) has illustrated a number of such variations in the Tremellales. By careful observation of the basidia of a series of fructifications belonging to almost any of the species it is easy to duplicate basidia such as he has shown and to add others. Brefeld speaks scornfully of Tulasne's illustration of the basidia of *Phlogiotis Helvelloides* in which they are shown as 2-celled, but it is possible to find fructifications of that species in which practically all basidia are 2-celled, although 4-celled basidia predominate in most collections. Reference has already been made to the variation in *Patouillardina*, in which some of the basidia in almost any mount will approach those of *Auricularia*. I have illustrated comparable irregularities in *Coleosporium*, generally regarded as a primitive rust. Many other instances could be adduced. It is, of course, true that similar aberrations may sometimes be observed in Homobasidiomycetes, but they are far less common and are usually associated with some environmental disturbance, such as exposure to cold while the basidia are maturing.

If the parasitic habit in Basidiomycetes is primitive and the saprobic habit derived, then, as Rogers (26) points out, the transition from parasitism to saprobism must have occurred many times and independently. Linde[illegible]s this easy to believe. I agree with Rogers in [illegible] reverse process much more

comprehensible, particularly when large and morphologically coherent groups of species are uniformly parasitic. This is not to deny that occasional reversals may have occurred, but such reversals would be expected, if anywhere, among the relatively unspecialized parasites capable of attacking a wide range of hosts and of living for long periods saprobically. In the series which I should assume ends rather than begins with the rusts, the transition from saprobic genera through such weak or occasional parasites as may be found in *Auricularia, Cystobasidium* and *Helicobasidium* to strong parasites such as *Herpobasidium, Eocronartium* and *Jola* leads by very close stages to *Septobasidium* and the rusts. The rusts, as a whole, comprise a highly specialized group, evidenced by their striking adaptation to limited host ranges and by the complicated life cycles which are particularly characteristic of what are regarded as the more primitive representatives of the order.

In general, the development of a parasitic habit is associated with the presence of a vesicular probasidium, serving as a storage organ until conditions are favorable for the formation of the spore-bearing outgrowth or epibasidium. Sometimes this is thin-walled, as in *Eocronartium, Jola* and *Herpobasidium;* sometimes the walls are slightly thickened, as in *Cystobasidium;* sometimes definitely thick-walled, as in many species of *Septobasidium.* The structure reaches its climax in the rusts, where the thick-walled probasidia may be borne singly or grouped in characteristic clusters of fixed form, constituting the compound teliospores. In this feature, as in others, there are some exceptions. All variations occur in *Septobasidium,* and a well-developed hypobasidium is found in *Helicogloea,* in at least one species of *Platygloea* and in *Neotyphula,* all of which are, so far as known, saprobic.

Germination by repetition is characteristic not only of the great majority of the Heterobasidiomycetes, including the rusts and smuts, but also of a limited number of the lowest Homobasidiomycetes. In many species of the Tremellaceae it exists side by side with the capacity to form blastospores or conidia. Only in the Dacrymycetaceae does it seem to have been completely replaced by the latter method. These facts justify us in regarding it as a primitive character which has been retained by advanced

Heterobasidiomycetes but discarded by all but a few Homobasidiomycetes.

In the Tremellales we find a striking preponderance of those features—relative simplicity of basidiocarp, heterogeneity of basidia, saprobism, germination by repetition—which may be taken as indications of a primitive position among the Basidiomycetes. Within the Tremellales, the considerations which may be advanced for regarding the *Tulasnella* basidium as representative of a basic type have been clearly stated by Rogers (26). Without repeating his arguments, except insofar as much of the present discussion must inevitably reflect them, it may be said that the not inconsiderable addition to our knowledge of the lower Basidiomycetes which has been made during the decade since his paper appeared has strengthened the position there upheld, modifying it in some respects, clarifying it in others. From the Tulasnellaceae as a center we may trace four almost complete series, three of them leading directly or indirectly to other families of the order and through the Auriculariaceae to the rusts and, less clearly but highly probably, to the smuts, and the fourth to such morphologically simple and hypothetically primitive thelephores as *Pellicularia* and thence to other members of the *Corticium*-complex and the remaining Homobasidiomycetes. Such a picture agrees with the known facts and makes more adequate provision for the transitional forms than the systems which are in current use. Its greatest weakness is its failure to point to any close and convincing connection with the Ascomycetes. In view of the large number of species of Basidiomycetes and the wide geographical distribution of many of them, it seems highly probable that the class is very ancient and that the development of the basidium took place in the remote past. Even so, the discovery during the past half century of so many significant connecting links within the Tremellales permits us to hope that we may eventually secure clearer evidence concerning their source than has yet been presented.

The accompanying chart (FIG. 1) attempts to present in graphic form the relationships I have suggested. The genera named are those through which transition to a neighboring family is suggested. They are all sufficiently well known to give reasonable

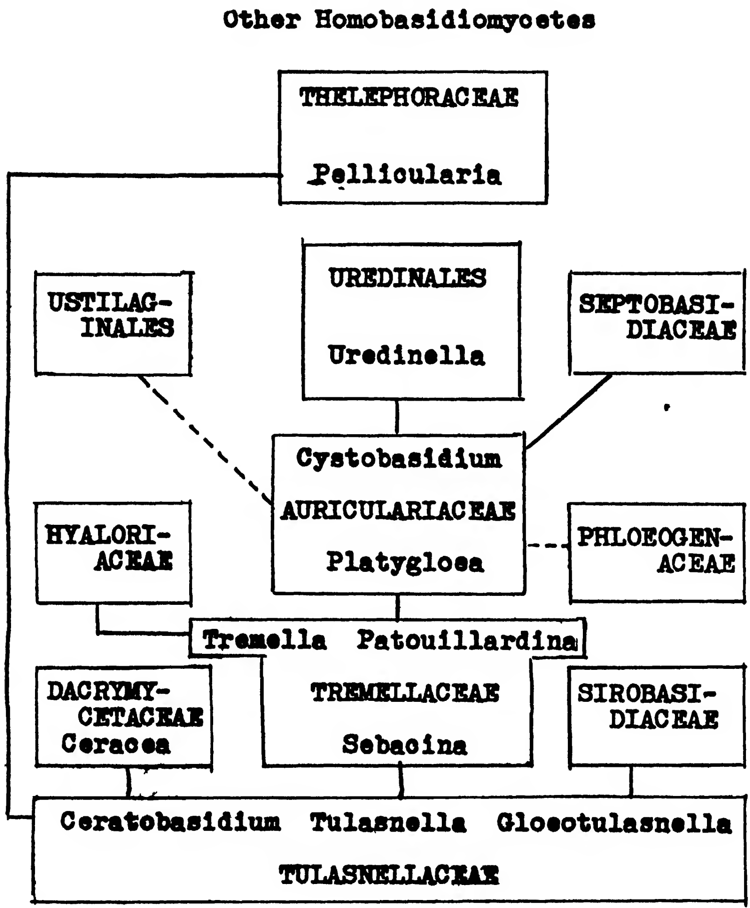

FIG. 1

assurance that the interpretation of their morphology is correct. It seems clear that the reality of these transitions must, in most cases at least, be recognized. It is true that a connected scheme of this sort remains connected no matter which group is placed at the bottom. Linder has presented the case for starting with the rusts. I have presented the case for the only reasonable and, in my opinion, the preferable alternative. Whether it be accepted or rejected, this discussion will have served its purpose if it leads to greater interest in the reclassification of the Basidiomycetes.

STATE UNIVERSITY OF IOWA,
IOWA CITY, IOWA

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A NEW DACRYMYCES–LIKE PARASITE OF ARUNDINARIA

LINDSAY S. OLIVE [1]

(WITH 35 FIGURES)

Recently, an unusual *Dacrymyces*-like fungus, parasitic on the leaves of *Arundinaria tecta* (Walt.) Muhl., was received by the Division of Mycology from the Bureau of Entomology and Plant Quarantine. Mr. John A. Stevenson, recognizing the unique nature of the fungus, turned over to the writer two collections of it which he had received. Both specimens were collected in November of 1943, one at Savannah, Georgia, and the other at Aurora, North Carolina.

On looking over the list of fungi reported on *Arundinaria tecta* in Seymour's Host Index, the writer found the name of *Dacrymyces epiphyllus* Schw. listed among the parasites of this plant. A check-up on the report has disclosed several interesting facts. In 1832, Schweinitz (Syn. Fung. Am. Bor., No. 1130, p. 186) applied the name, *Dacrymyces epiphyllus*, to a fungus which he believed to be parasitic on the leaves of *Galium*. A study of a portion of the type collection of Schweinitz' fungus in the Mycological Collections of the Bureau of Plant Industry has shown that the host is not *Galium*, but *Euthamia graminifolia* (L.) Nutt. The writer has found, upon further investigation, that the parasite is not a *Dacrymyces*, but is the telial stage of *Coleosporium delicatulum* (Arth. & Kern) Hedgc. & Long. The little yellow, gelatinous, telial pustules had been mistaken by Schweinitz for a *Dacrymyces*.

This finding made it obvious that the report of *Dacrymyces epiphyllus* on *Arundinaria tecta* was also a mistake. Through the kindness of Dr. David H. Linder, we were able to obtain from the Farlow Herbarium Index the source of this report. In a list of

[1] Pathologist, Emergency Plant Disease Prevention Project, Bureau of Plant Industry, Soils, and Agricultural Engineering, United States Department of Agriculture, Beltsville, Maryland.

Alabama fungi compiled in 1897 by G. F. Atkinson (1), the following note was found: "*Dacryomyces epiphyllus?* On leaves of *Arundinaria tecta.* Auburn *2327,* Nov. 3, 1891." The question mark indicated Atkinson's uncertainty about the validity of his identification. This same report occurred again, without the question mark, in Mohr's *Plant Life of Alabama* (Contrib. U. S. Nat. Mus. **6**: 196. 1901).

At the writer's request, Dr. H. M. Fitzpatrick sent from the Mycological Collections at Cornell University a portion of what appears to be Atkinson's only collection of this fungus on *Arundinaria tecta.* The parasite proved to be identical with the one described here. Investigations have shown that the fungus possesses certain characteristics which clearly indicate that it belongs in the Dacrymycetaceae. However, it is equally obvious that the organism is quite distinct from any other genus in that family. It is here described as a new genus and a new species.

Dicellomyces gen. nov.

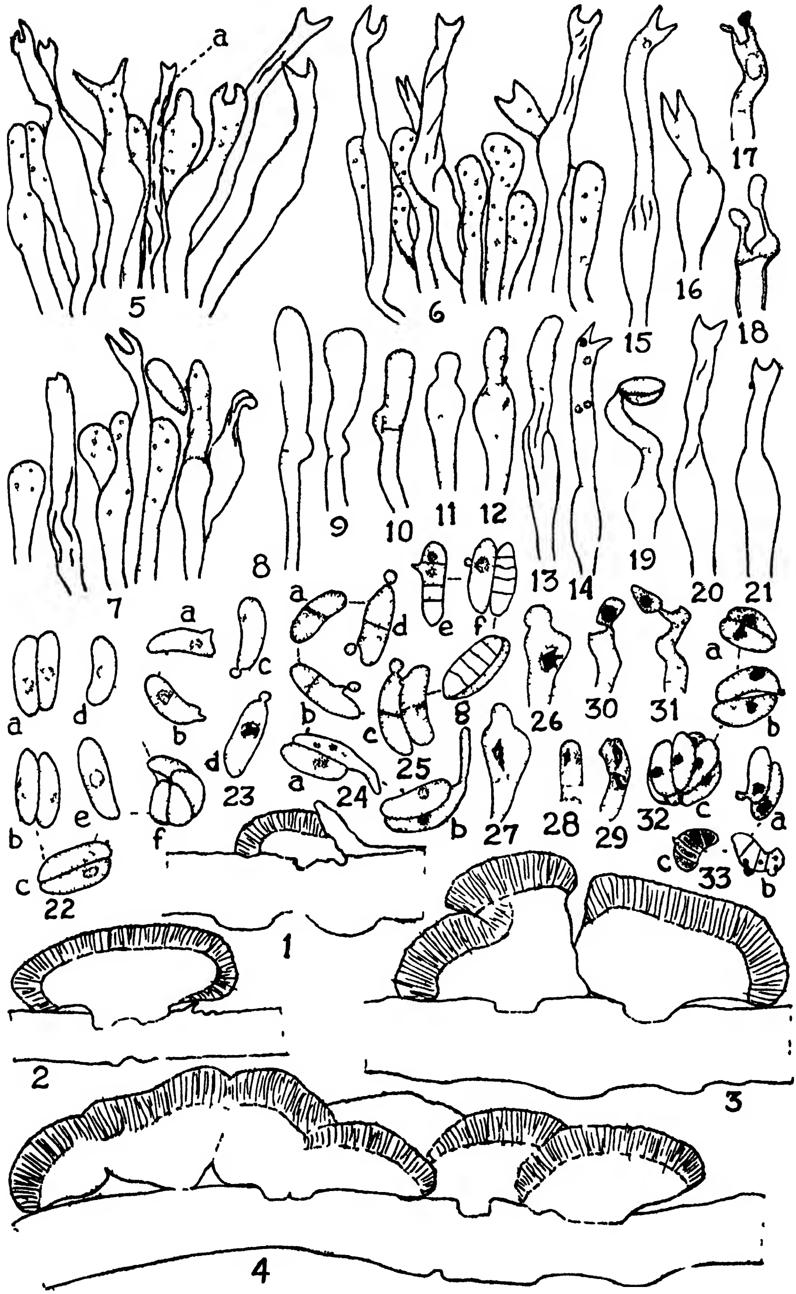
Fructificationes in foliis parasiticae, parvae, flavae, firme gelatinosae, pulvinatae usque subdisciformes, in textura folii basi obtusa insertae; basidia e probasidiis tenuibus persistentibus oriunda, extra superficiem fructificationis producta; sterigmata dua, comparative brevia; basidiosporae allantoideae, demum septatae, sporidia parva, globosa gerentes.

Type species *D. gloeosporus.*

Leaf parasite; small, yellow, firmly gelatinous, pulvinate to nearly discoid, with a blunt base inserted into the leaf tissue; basidia arising from thin-walled, persistent probasidia and produced externally to the surface of the fructification; sterigmata 2, becoming septate, producing small, globose conidia.

Dicellomyces gloeosporus sp. nov.

Fructificationes hypophyllae in maculis decoloribus, parvae, flavae, firme gelatinosae, pulvinatae usque subdisciformes, in substrato basi obtusa insertae, hyphis in folium penetrantibus, 440–700 × 485–955 μ, 194–353 μ altae, in aetate nigrobrunnescentes et collapsae; hymenium superficiem superiorem totam fructificationis tegens, e probasidiis 4.1–6.3 μ in diam., dense compactis, longe pedicellatis, clavatis vel subpyriformibus basidia gerentibus compositum; basidia angusta, in longitudinem variabilia, 2.4–4.1 × 9–25.2 μ, extra superficiem gelatinosam producta, sterigmata dua, comparative brevia, 1.8–4.0 μ longa gerentia; basidiosporae allantoideae, 2.7–4.5 × 8.6–11.9 μ, in paribus



FIGS. 1–33. *Dicellomyces gloeosporus*. Microscopic characters.

adhaerentibus productae, paribus pluribus saepe in globulam conglutinosis, apiculo non evidente, frequenter 1–4-septatae, saepe gemmantes et sporidia parva, subglobosa gignentes.

In foliis *Arundinariae tectae.*

Fructifications hypophyllous, on discolored spots, small, yellow, firmly gelatinous, pulvinate to nearly discoid, with a blunt base inserted in the leaf, hyphae penetrating into the leaf tissue, measuring 440–700 × 485–955 μ and 194–353 μ tall, becoming dark brown and shrunken with age; hymenium covering entire upper surface of the fructification, composed of closely packed, long-stalked, clavate to nearly pyriform probasidia, 4.1–6.3 μ in diameter, the latter persistent and giving rise to narrow basidia of varying lengths; basidia 2.4–4.1 × 9–25.2 μ, produced externally to the gelatinous surface, giving rise to 2 relatively short sterigmata, 1.8–4.0 μ in length; basidiospores allantoid, 2.7–4.5 × 8.6–11.9 μ, produced in adherent pairs, several pairs often clinging together in a ball, apiculus not apparent, basidiospores frequently becoming 1–4-septate, often budding out small, more or less globose, conidia.

On leaves of *Arundinaria tecta* (Walt.) Muhl., Savannah, Georgia, November 9, 1943, A. W. Blizzard, **type**; Aurora, North Carolina, November 12, 1943, C. S. Tuthill.

The first symptoms of the parasite on its host are the appearance of small yellow spots on the leaves. These spots enlarge and become dark brown, usually with a surrounding yellow area. The small yellow fructifications can be seen on these discolored areas. Eventually, large portions of badly diseased leaves may become brownish and dead. The spots show up with about equal clarity on both surfaces of the leaf. In figure 34, the upper surface of the first two leaves (*a* and *b*) and the lower surface of the third leaf (*c*) are shown.

The fructifications appear only on the lower surface of the leaves and look much like a minute *Dacrymyces* (FIG. 35). These sporocarps are bright yellow when dry, but become a lighter shade of yellow on being soaked. There is about a 30–50 per cent expansion when they are placed in water.

The fructifications arise singly or in groups which often anastomose (FIGS. 1–4, 34, b). The young sporocarp arises from within the leaf and, as it enlarges, ruptures the overlying epidermis (FIG. 1). Transverse sections of the leaf in the diseased areas show that the sporocarp is attached within the leaf by a blunt base.

These sections also show that the fructification is composed of an inner sterile tissue and an outer hymenial layer which covers most of the exposed surface (FIGS. 1–4).

The structure of the hymenial layer appears to be different from that described for any other member of the Dacrymycetaceae. The hymenium is composed entirely of long-stalked, clavate to nearly pyriform probasidia embedded in the gelatinous substance of the fructification. Sometimes clamp-like processes were seen at the bases of the probasidia (FIGS. 8–10), but such structures were generally difficult to make out in this material. The probasidia, upon germinating, produce narrow basidia of varying lengths which come to lie entirely outside the gelatinous surface (FIGS. 5–7). The probasidia empty all their protoplasmic contents into the basidia and remain distinct for some time afterwards (FIGS. 5–21).

The mature basidium is terminated by 2 sterigmata which are decidedly shorter than those of any other fungus described for this family. Of course, these sterigmata do not have to perform entirely the same functions as the longer ones of other Dacrymycetaceae; that is, they do not have to extend through a gelatinous layer in order to bring the basidiospores to the surface. Each basidium produces two basidiospores, which, as they enlarge at the tips of the sterigmata, come together along their inner surfaces and adhere (FIGS. 17–19). They are always shed in adherent pairs (FIGS. 22, *a, b, c;* 32, *a, b*), or several approximate pairs may cling together in agglutinated balls (FIGS. 22, *f;* 32, *c*). They are probably not discharged forcibly from the sterigmata. Although these spores are rather strongly adherent, some of them eventually become separated, as many of the figures show. They are allantoid in shape and without apiculi. After sporulation, basidial and probasidial walls may remain expanded, but eventually they both collapse (FIGS. 5*a*, 7).

Most of the material examined was mounted in a phloxine preparation, after which nuclei could generally be made out within the basidiospores. The spores are at first uninucleate. Later they become septate and multinucleate. While they are unicellular, they may bud out tiny globose conidia (FIG. 23), or they may sometimes produce slender germ tubes (FIG. 24). Frequently

they become 1–4-septate and bud out conidia in a manner typical of *Dacrymyces* (FIG. 25).

Although none of the material used in the present investigation was alive, some of it was carried through a nuclear staining

FIGS. 34, 35 *Dicellomyces gloeosporus* on leaves of *Arundinaria tecta*.

technique as for live material. A few pieces of a diseased leaf containing some of the fructifications were placed in chromic-acetic-osmic acid solution. Later they were imbedded in paraffin and sectioned, and the sections were stained with the iron-alum haematoxylin procedure. Conclusions based on a study of such

material must, of course, be made with caution, since nuclear phenomena are easily confused with numerous artifacts which are generally present. However, a few important details were obtained from a study of this material.

The main purpose of this cytological investigation was to determine the orientation of the spindles during meiosis. Indications are that the first division is in progress before the nucleus has passed from the probasidium into the developing basidium (FIGS. 26, 27), and that there is a second division in the basidium (FIGS. 28, 29). The few spindles observed seemed to be parallel to the long axis of the basidium Thus it appears that the fungus is truly phragmobasidial in nature, as one might have expected from its obvious relationship to other Dacrymycetaceae.

More clearly in evidence than any other cytological detail was the uninucleate condition of the basidiospores (FIG. 32). Each spore receives a single nucleus when it is produced (FIGS. 30, 31). A few spores, unicellular and septate ones, were observed producing conidia (FIG. 33).

The important characteristics of *Dicellomyces* which seem to justify its being considered a new genus of the Dacrymycetaceae, distinct from all other genera of that family, may be summarized as follows: (1) its parasitic nature on a seed plant, (2) the presence of persistent probasidia, (3) basidia produced externally to the gelatinous hymenium, and (4) relatively short sterigmata. The fungus is placed in the Dacrymycetaceae on the basis of (1) its characteristic yellow, firmly gelatinous sporocarps, (2) 2-sterigmate basidia, (3) phragmobasidial nature, and (4) basidiospores which may become septate and which may bud out small, globose conidia.

The present fungus seems to exhibit several interesting similarities to and parallelisms with other groups of fungi. The development of a slender, 2-sterigmate basidium from a persistent probasidium and the parasitic nature of the fungus are characteristics which are found in *Brachybasidium Pinangae* (Rac.) Gäum. The fruiting bodies of the latter appear as numerous small, hemispherical bodies which emerge from the stomata on the underside of *Pinanga* leaves. They appear to consist entirely of a few probasidia which give rise to slender 2-sterigmate basidia in a manner

similar to that described for the present fungus. Although no reference was found concerning the texture of these fructifications, either in Raciborski's (4) original description of the fungus, or in Gäumann's (2) later treatment of it, the present writer finds that the probasidia seem to be held together by a gelatinous substance, which is more in evidence when some of the material is soaked in water. Apparently, the only outstanding morphological difference between the fructification of *Brachybasidium* and that of *Dicellomyces* is the absence of the sterile sub-hymenial tissue in the former.

On the other hand, Gäumann (2) has shown, in a limited cytological investigation of *Brachybasidium Pinangae,* that the meiotic spindles in the developing basidium are at right angles to the long axis of the basidium. This chiastobasidial nature of the fungus and the presence of a *Dacrymyces*-like basidium arising from a distinct and persistent probasidium make a peculiar combination. However, Gäumann mentions several times in his discussion the difficulty which he experienced in trying to obtain material with clear cytological details, and it may be that his figures were misinterpreted on this account. The later development of the basidiospores after they are shed is not described..

If *Brachybasidium* should prove definitely to be chiastobasidial, it is not likely that the fungus can be considered closely related to *Dicellomyces.* On the other hand, if it should prove to be phragmobasidial in nature, only a reduction in the size of the *Dicellomyces* type of fructification would be required to derive that of *Brachybasidium.*

From the standpoint of its parasitic nature and persistent probasidia, *Dicellomyces* appears to occupy a position in the Dacrymycetaceae similar to that held by such genera in the Auriculariaceae as *Iola* and *Herpobasidium,* which are also parasitic on higher plants and have persistent probasidia. Since both families are composed primarily of saprophytic fungi, which generally have no distinct resting phase in the development of the basidium from the probasidium, the combination of these two characters is exceptional. From the standpoint of phylogeny in these two families, such forms are of the greatest importance. They emphasize the probability of the origin of these groups from

rust-like ancestors. The present fungus must have had its origin either in a rust-like ancestor which possessed persistent probasidia, or from a parasitic ancestor which had inherent within it the tendency to produce resting probasidia and from which other heterobasidiomycetes, including the rusts, might also have evolved.

In the light of the above discussion, it would seem less likely that the *Dacrymyces* type of basidium can be derived from the *Corticium sterigmaticum* type, as Rogers (**5**) has suggested. Moreover, it would appear that the latter's consideration of the resupinate *Ceracea* type of fructification as the most primitive in the Dacrymycetaceae is no longer well founded. On the other hand, the present investigations tend to add support to the theory held by Linder (**3**) that the Dacrymycetaceae were evolved from rust-like ancestors and that the pustulate fructification preceded the resupinate in the evolutionary development of the group. The present writer would not, however, entirely eliminate the possibility of an origin from a rust-like ancestor which already possessed resting probasidia. Linder's selection of the *Coleosporium*-like ancestor for his starting point in the derivation of the dacrymycetaceous line does not permit this possibility, but at the same time does not preclude the possibility that a derived form may have inherited the tendency towards the production of persistent probasidia.

SUMMARY

1. A leaf parasite of *Arundinaria tecta,* representing a new genus and species, has been described. The name *Dicellomyces gloeosporus* is proposed.

2. The fungus resembles *Dacrymyces* in its color, form of fructification, gelatinous nature, 2-sterigmate basidia, and allantoid basidiospores which may become septate and which frequently bud out globose conidia.

3. It differs from all other genera of the Dacrymycetaceae in its persistent probasidia, basidia produced externally to the gelatinous matrix, and relatively short sterigmata.

4. The parasitic and phragmobasidial nature of the fungus and its possession of persistent probasidia are believed to be primitive

characteristics which point toward the origin of the group from rust-like ancestors.

The author is grateful to Miss Edith Cash for her preparation of the Latin diagnosis, and to Dr. C. L. Lefebvre, of the Forage Crops Division, for the use of his staining facilities. The author also appreciates the assistance of Dr. Charles Drechsler in helping him select an appropriate name for the fungus.

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EXPLANATION OF FIGURES

FIGS. 1–33 (All figures × 945, except 1–4, × 66). Microscopic characters. 1, Young fructification breaking through lower epidermis of leaf of *Arundinaria tecta*, hymenium represented by striations; 2–4, fructifications on lower surface of leaf, some anastomosing; 5–7, details of the hymenium, showing probasidia and basidia, *a*, collapsed basidium and probasidium; 8–10, probasidia with clamp-like processes; 11–16, development of the basidia (Note the emptying of the probasidia); 17–19, development of the basidiospores, figure 19 showing 2 agglutinated spores; 20 and 21, empty probasidia and basidia; 22, basidiospores, *a, b, c*, typical agglutinated pairs, *c, d*, single spores, *f*, agglutinated ball of spores; 23, unicellular basidiospores producing conidia; 24, basidiospores producing germ tubes; 25, septate basidiospores, some producing conidia; 26–33, cytological details: 26 and 27, beginning of first meiotic division in the probasidia; 28 and 29, second meiotic division in the young basidia (Note orientation of spindles); 30 and 31, development of uninucleate basidiospores; 32, uninculeate basidiospores, *a* and *b*, typical agglutinated pairs, *c*, agglutinated ball of spores; 33, basidiospores producing conidia.

FIGS. 34, 35. Appearance of fungus on the host. 34, Leaves of *Arundinaria tecta*, showing leaf spots caused by the fungus, *a* and *b*, upper leaf surface, *c*, lower surface, natural size; 35, appearance of the fructifications on the lower surface of the leaf in moistened material, × 10.

THE SIGNIFICANCE OF ZYGOSPORE CHARACTER IN POLYPHAGUS EUGLENAE

A. F. Bartsch

(with 23 figures)

Polyphagus Euglenae Nowak. is perhaps one of the most intensively studied species of the aquatic Chytridiales and has been known since the early collection by Gros (**1851**) who was unaware of the true nature of the organism which he described and figured. It has been reported since that time from all parts of Europe, from Asia and the United States and perhaps is cosmopolitan at least in the northern hemisphere. The life history of this form is quite completely known from the excellent and intensive researches of Nowakowski (**1876, 78**), and knowledge of its cytological and morphological development has been supplied by Dangeard (**1900–01**) and by Wager (**1898, 1899, 1913**). In spite of this intensive investigation into the details involved in the parasitism, growth and sexual and asexual modes of reproduction, controversies have arisen concerning some of the fundamental points involved in the life history. Some of these relate to the phototactic nature of the zoospores (Wager, **1913**), the function of sexually differentiated zoospores in determining the development of an incipient thallus into a functional male or female gametangium (Kniep, **1928**), the significance of the formation of two kinds of zygospores which differ primarily in possessing or lacking an ornamented exospore (Nowakowski, **1876, 78**; Dangeard, **1900–01**; Wager, **1913**; Sparrow, **1936, 43**), and the validity of reports of the occurrence of two distinctly different processes in the formation of the zygospores (Nowakowski, **1876, 78**; Wager, **1913**; Dangeard, **1900–01**). The present study is concerned primarily with the relationship of the two kinds of zygospores found in this fungus and with the methods involved in their formation.

Occasionally there have appeared in mycological literature reports of finding two kinds of zygospores in *P. Euglenae*. These spores are reported to differ from each other mainly in the possession of a smooth exospore in the one type and a spiny one in the other. In the accounts of early collection and culture of this fungus, the presence of both types led to speculation concerning their relationship. The fact that all vegetative thalli were more or less similar in all apparent respects led some to believe that the zygospore differences are not of specific significance and that whatever differences were found in the vegetative thalli represented the anatomical variation between specimens within the species. This apparently is the view held by Nowakowski in 1876 because he suggested that the ornamented type is normal and that the smooth type is the result of abnormal development under poor nutritional conditions. He also reported that the smooth form is produced as the result of communication by the tip of a male conjugation tube with the already extruded contents of a female thallus. In addition, he suggested that it may be formed as the normal zygospore of a distinct "race" of *P. Euglenae*. Two years later (**1878**), however, and after additional study of the smooth type, he stated that his previous report on the method of smooth zygospore formation is erroneous and based upon the study of an insufficient number of specimens. He concluded, in addition, that the fungus is distinct from the spiny form and described it under the trinomial, *P. Euglenae* var. *minor*. This was done on the basis of the smaller size of the vegetative thalli and apparently on the assumption that the smooth character of the zygospore wall is constant. There is no evidence that this conclusion was based upon the observation of unifungal cultures through a number of generations although he (**1878**) refers to its collection in a street gutter at Lwów as if it occurred there by itself.

Dangeard (**1900–01**) also found both types of zygospores in his cultures and, apparently unaware of Nowakowski's later paper (**1878**), adopted his earlier view that the wall differences are the result of nutritional influences. Wager (**1913**), in studying the cytology of *P. Euglenae,* was inclined to agree with Dangeard. Sparrow (**1936**) collected *Polyphagus* in Denmark and Britain. He found, in the Danish material, that only the spiny type of

zygospore was present; in the British collection both were present, but the smooth form was predominant. He also examined de Bary's slides from the British Museum (N.H.), labelled "Mai, 1876, glyc. Nowakowski." These specimens, which Sparrow points out can certainly be considered a co-type of the fungus, bore both the spiny and the smooth types of zygospores. In commenting on these zygospore findings, Sparrow (**1936**, **43**) expressed the belief that future cultural studies will establish the existence of two distinct species parasitizing *Euglena*.

Because of this controversy, cultural methods have been used in a study of this fungus in order to determine whether *P. Euglenae* characterized originally by Nowakowski and later by others constitutes a single species or whether it and *P. Euglenae* var. *minor* represent two distinct species with somewhat similar thalli and dissimilar zygospores. During the spring of 1941 and again in the fall of 1944 collections of *Euglena* were made in farmyard puddles and other likely habitats in order to obtain material for this study. Thalli of the fungus appeared within three or four days in material collected at the following four sites:

A. Farmyard puddle near Holy Hill, Wisconsin, March 8, 1941.
B. Farmyard puddle on Albert Wittl farm, highway U. S. 18, 3 miles east of Jefferson, Wisconsin, April 11, 1941.
C. Pool below artificial waterfall, Lake Park, Milwaukee, Wisconsin, June 4, 1941.
D. Farmyard puddle ½ mile east of Mapleton in northeast corner of Waukesha County, Wisconsin, November 13, 1944.

Cultures from these four collections were designated A, B, C and D respectively and are referred to hereafter under these designations. Liquid cultures were prepared by adding zoospores and thalli to growing cultures of *Euglena viridis;* these were maintained by adding *Euglena* cells from stock cultures at frequent intervals as required and by making transfers to fresh liquid cultures. Other cultures were obtained by growing the host on agar plates of synthetic medium, hereafter referred to as *Euglena* plates, and inoculating with zoospores of the fungus when the surface of the plate was well tinged with green. It was possible, with these two

methods, to keep vigorous stock cultures of A, B, and C until December, 1942 and of D until April, 1945.

In all vegetative stages the thalli in the four culture lines appeared somewhat similar and could not be distinguished from *P. Euglenae* as described and figured by Nowakowski (**1876**, **78**), Dangeard (**1900–01**) and Wager (**1913**). Since the anatomy and development of the vegetative stages are so well known from the excellent works of these early investigators, no detailed account is included here.

As each of the cultures became from three days to two weeks old and zygospores were produced, it was noted that differences existed in those formed in cultures A and C from those in culture B. These differences corresponded with those found between zygospores in single collection cultures by most students of this fungus. The zygospores of series A and C were similar in being smooth-walled while those of series B were spiny-walled and differed from the former in other additional characters as well. Both types of zygospores were found in culture D. In these cultivated specimens it was possible to follow the sequence of events leading to formation of both spiny and smooth zygospores. In no case was the latter formed by enlargement of the extruded contents of a female thallus following its fertilization by a male conjugation tube as described originally by Nowakowski (**1876**). Except for variation in detail, there is but a single conjugation process in which the zygospore is formed at the distal end of a delicate conjugation tube and in contact with or near the larger of the two thalli. The bulk of its body is composed of the protoplasmic contents of the two gametangia which flow to the tip of the conjugation tube where they become confluent and eventually are set off by distal and proximal septa. In formation of the spiny form the protoplasmic mass which represents the incipient zygospore assumes a subapical position in the conjugation tube so that it later is connected with each of the attached thalli by a tube. These observations therefore confirm Nowakowski's later description (**1878**) of smooth and spiny zygospore formation. He also pointed out at this time that the smaller thallus should be considered the female one since the mature zygospore wall is

formed by differentiation of a portion of its membrane—the conjugation tube wall. However, it is to be noted that the major volume of protoplasm in the zygospore is contributed by the larger thallus, that in both forms the mature zygospore either is sessile upon or lies close to the larger thallus and that the latter assumes a passive role while the smaller thallus assumes an active one in accomplishing conjugation. The writer concludes from these facts that, if sexual designations are to be applied, the more voluminous and passive thallus should logically be called a female gametangium or oogonium. This is the treatment in all accounts other than that of Nowakowski (**1878**), and it is being followed in this report.

Unifungal cultures were obtained by one or more of the following methods for each of the collection series, A, B, and C, and for the smooth (DM) and spiny (DS) forms of collections D. These methods were adapted from those used by Couch (**1939**) for the isolation of other chytridiaceous forms.

(1) Single zygospore culture:

A single isolated zygospore produced and lying on the surface of a *Euglena* plate was removed, along with a cylindrical agar plug, by manipulation of a 2 mm. circular cutting tool. This plug was placed on end on a microscopic slide, and after examination verified the presence of but a single zygospore on its circular upper surface, the plug was placed on its side to permit slicing off the upper ½ mm. as a disk bearing the inoculum. This disk was then transferred to a fresh *Euglena* plate and flooded with sterile charcoal water to induce germination.

(2) Multi-zoospore culture:

A single isolated zoosporangium growing on agar was removed, along with an agar plug, as in the method above and introduced into a hanging drop of charcoal water. After the sporangium matured and liberated zoospores, the latter were drawn up along with the liquid of the drop and distributed over the surface of a plate culture of *Euglena* by means of a finely drawn pipette.

(3) Single thallus culture:

A single isolated immature thallus growing on the surface of a *Euglena* plate was manipulated in the same manner as were the zygospores in method (1) above.

Replicates of these cultures were prepared by transferring inhabited blocks of agar to the surface of fresh *Euglena* plates. These replicates were then treated in such manner that any persistence of distinctive zygospore characters, as found to exist singularly in three of the four original cultures, could by no means be attributed to variations in the physical surroundings or to the nature of the nutritional supply. For the most part, these cultures were kept at room temperature and were subjected to intermittent daylight and darkness by virtue of their position at a south window. Culture series were rotated in horizontal and vertical positions from time to time. The smooth and spiny-walled isolates of collection D, which were studied when cultures A, B, and C no longer were available, were handled in a similar manner. It is assumed that the environmental conditions which prevailed during the period of study were not differentially involved in determining zygospore character. *Euglena viridis*, alone, was supplied as the host species for all cultures, and a single culture medium formula was used for all *Euglena* cultures at a given time.

Cultures A, B, C and D, as collected, were kept under observation for 21, 20, 18 and 5 months respectively while the unifungal isolates on agar of A, B and C were under observation concurrently for 13 months. The unifungal isolates of culture D were similarly kept under observation for 4 months. During these periods the zygospores in series A, C and DM maintained all those characters by which they were originally distinguished from those of series B and later from DS. Throughout the period of cultivation no mature smooth-walled zygospores were found in series B or DS, and likewise no spiny-walled ones were found in series A, C or DM. While it was noted that scarcity of food supply (*i.e.*, paucity of encysted *Euglena* cells) and decrease of water content in the agar caused successive groups of zygospores to be measurably smaller, still they were constant in the character of their type.

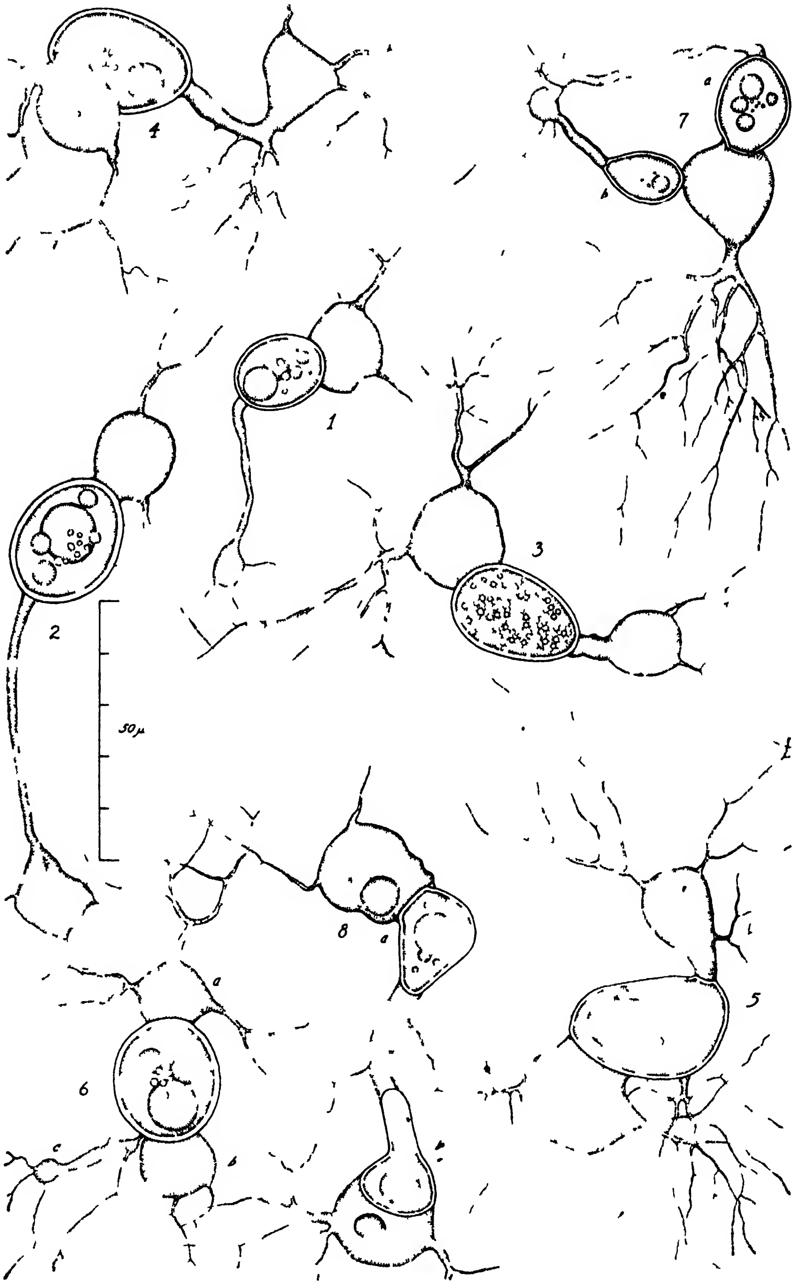
It seems apparent from these data, then, that the nature of the zygospore wall is a persistent and inherited character whose fundamental features are influenced little if at all by environmental conditions. It is concluded that the smooth type is not abnormal and its exospore character is not the result of poor nutritional conditions. In addition to the presence or absence of spines on the surface of the exospore, the zygospores differ from each other in a number of additional features. These differences are shown in table I.

TABLE I

ZYGOSPORE CHARACTER IN CULTURAL ISOLATES

	Isolates: A, C and DM	Isolates: B and DS
Shape	Spheroid, ovoid, elongated, reniform, lacrymoid, clavate, constricted, truncated; considerable irregularity in shape.	Spheroid, ovoid, wide-fusiform; quite regular in shape.
Length	19.6–35.0 μ, av. 26.2 μ	18.0–27.0 μ, av. 22.6 μ
Width	14.0–28.2 μ, av. 19.7 μ	10.6–26.3 μ, av. 17.9 μ
Location	Typically sessile on female thallus; attached to male thallus by a tube.	Typically attached to female thallus by a tube, rarely closer to it than 4.9 μ, as far from it as 13.2 μ, av. 8.9 μ; attached to male thallus by a tube.
Wall	Two-layered; exospore and endospore smooth and hyaline.	Two-layered; exospore always more or less spiny, bright yellow to amber; endospore smooth and hyaline.

As indicated in table I, the two types of zygospores, with their attached antheridial and oogonial cases, can be distinguished with ease by microscopic inspection. It is to be noted that, while the two forms have been referred to as the "spiny" and the "smooth," they are differentiated by the possession and constancy of other additional characters. The smooth form has never been seen to possess a tube connecting it with the empty oogonial case as in the spiny form (FIG. 12, a), although some specimens appear almost to possess one because of the constriction of the attachment region (FIG. 4). Although it is possible that the spiny form may lack this tube under conditions of extreme crowding of the thalli, none has been seen in cultures of this material.



FIGS. 1–8. *Polyphagus laevis.*

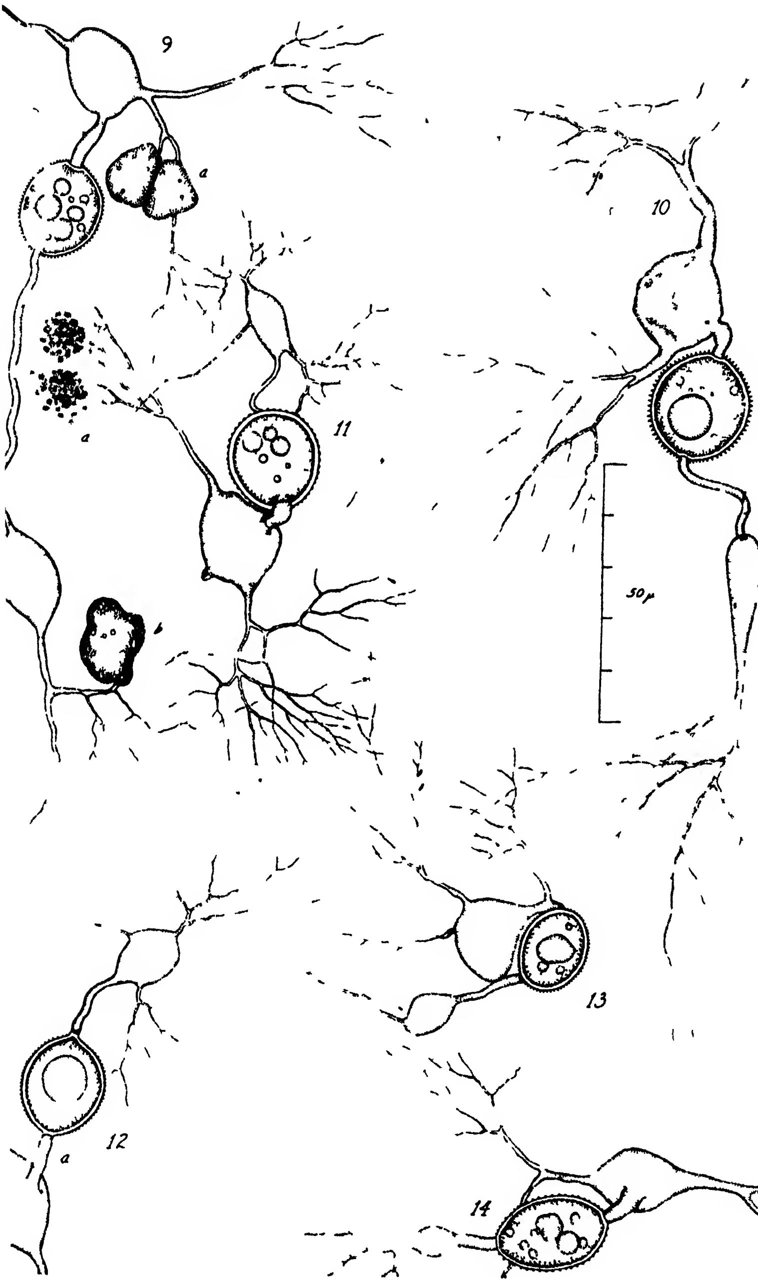
While the thalli illustrated in figures 1 and 2 may be considered typical (*i.e.*, found to be most common in culture), all of the thalli shown in figures 1–8 indicate the basic character of this type. Here, the endospore and exospore are poorly differentiated since both are smooth and hyaline, but at times one may find spores having a faint bluish-green, and more rarely a yellowish tinge. The oleaginous globules, so characteristic as a nutritional reserve, are variable in size and number, but generally there are four or five large globules and a variable number of small ones (FIGS. 1, 2, 6, 7 a). An occasional zygospore becomes completely filled with globules of uniform size, and the cell contents then appear quite dense (FIG. 3). The remainder of the zygospore content is hyaline, homogenous, watery and devoid of granules of appreciable size.

The zygospores shown in figures 1–8 have been selected from cultures A, C and DM as representatives of various developmental types. Figures 1 and 2 show the result of conjugation between a small thallus and a larger one lying at some distance from it. Frequently the zygospore is truncated at its point of contact with the oogonium (FIGS. 7a, 8a). Obviously, in this type, only a small distal portion of the conjugation tube has become intimately involved in the formation of the zygospore, and the remainder has not become inflated. Figures 3 and 5 show the type of development which follows when the antheridium and oogonium lie closer than those referred to above. While a portion of the conjugation tube is still recognizable, the major part of it has become involved in the formation of the zygospore, and the remainder is more or less inflated. The thalli shown in figures 4 and 6 indicate the course of development when the antheridium and oogonium are of similar size. In the first of these (FIG. 4), however, a conjugation tube bearing rhizoids is apparent and indicates the antheridial character of the attached thallus case. When the conjugation tube has become completely inflated in formation of the zygospore (FIG. 6), it is impossible to recognize the sexual nature of thalli such as *a* and *b*. This type of configuration is common and results from the proximity of immature thalli at a time when environmental conditions stimulate sexual reproduction. Thallus *c*, which still possesses protoplasmic contents, apparently has no con-

nection with the conjugating thalli or the zygospore but merely began development in the same locality in the medium.

In addition to the mildly aberrant courses of development described above, a number of abnormal ones have been observed. These have to do with the functioning, in a double capacity, of one or the other of the gametangia. In some instances it appears that an oogonium may be receptive to the tips of the conjugation tubes from two male individuals resulting in the formation of two zygospores attached to the surface of a single female thallus (FIG. 7). Although zygospore *a* is larger than *b*, no fundamental difference between them could be noted by microscopic examination. In other instances evidence was seen to suggest a multiple function by a male thallus (FIG. 8). Although the history of these two zygospores is unknown, the tubular portion between them is interpreted as the visible remains of a male thallus from which a conjugation tube had contacted each female thallus at *a* and *b*. It is curious that oleaginous globules were excluded from the zygospores, one remaining in each of the oogonia. Unfortunately the nuclear history in these two types of abnormality is unknown. From the cytological study of Wager (**1913**) it is known that nuclear divisions occur only in the sporangia; it seems inconceivable, then, that the female thallus of figure 7 and the male thallus of figure 8 should be conveniently provided with a nucleus for each zygospore. It appears more probable that one of the apparent zygospores in each case is a parthenogenetic structure comparable to the cysts produced by the prosporangia but differing fundamentally from the latter in having received nutriment by connection with a female thallus.

In contrast to the smooth form, the exospore of the spiny one varies in color from bright lemon to deep amber and sometimes brown, with some evidence from delicate focusing under high magnification to suggest that the core of the spine is more hyaline than its shell or that the endospore extends into the spine as a hyaline core. The spines, themselves, vary from short, delicate ones which are typical (FIG. 13) to relatively coarse, conical projections (FIG. 10); occasionally the ornamentation may appear as somewhat scattered spines (FIG. 14) and rarely as rounded, short bullations (FIG. 11). Frequently the spines are shorter and more



FIGS. 9–14. *Polyphagus Euglenae.*

delicate at the two ends of the zygospore than over its equatorial region (FIG. 12). The nutritional reserve usually is confined in one or two relatively large globules with a number of additional small ones (FIGS. 10, 12–14). In addition, the cytoplasmic contents appear quite granular and dense although this appearance is enhanced to a considerable degree by diffraction of the light in passing through the upper and lower spine-bearing layers. While usually the constituents of the host cells have been reduced at this stage to an irregular mass of clumped, reddish-colored granules (FIG. 11a), an occasional fungus will be found to attack new *Euglena* cysts late in its course of development so that the host contents are not fully utilized (FIGS. 9a and b).

Some variation in the details of zygospore formation has been noted in this form, but the extremes of variation and the so-called abnormalities, which are common in the smooth form, are strikingly absent. Although the presence of a number of zygospores on the surface of an oogonium has not been seen in this material, it has been noted and figured for the spiny type by Nowakowski (1878).

The thallus-zygospore relationship shown in figure 12 has been found to be most common, although the configurations shown in figures 9 and 10 are almost equally prevalent. The predominant type of oogonium is fusiform with a laterally attached communication tube (FIGS. 10–12, 14); other shapes have been seen occasionally (FIGS. 9, 13). The antheridia exhibit considerable variation in shape from fusiform or ovoid with one rhizoidal axis (FIGS. 9, 10, 13, 14) to a more or less irregular shape with several rhizoidal axes (FIGS. 11, 12).

From the foregoing it is apparent that these two fungi can be distinguished with ease during and after the process of conjugation. Upon studying thalli in the vegetative stages, it was found that here, too, they differ sufficiently to permit positive identification. The prosporangia in cultures B and DS are typically fusiform or clavate with an elongated or cylindrical zoosporangium attached in a lateral position (FIGS. 17, 18). Globose prosporangia (FIGS. 15, 16) were fairly common. Frequently the zoospo-

rangium was found to be somewhat elongated with an undulated surface (FIG. 16) and occasionally one was found to be considerably elongated (FIG. 15). The vegetative thalli in cultures A, C and DM characteristically consist of a globose prosporangium and a globose (FIGS. 19, 21, 22), ovoid (FIG. 23) or curved (FIG. 20) zoosporangium. Generally the thalli of this type are smaller and more delicate.

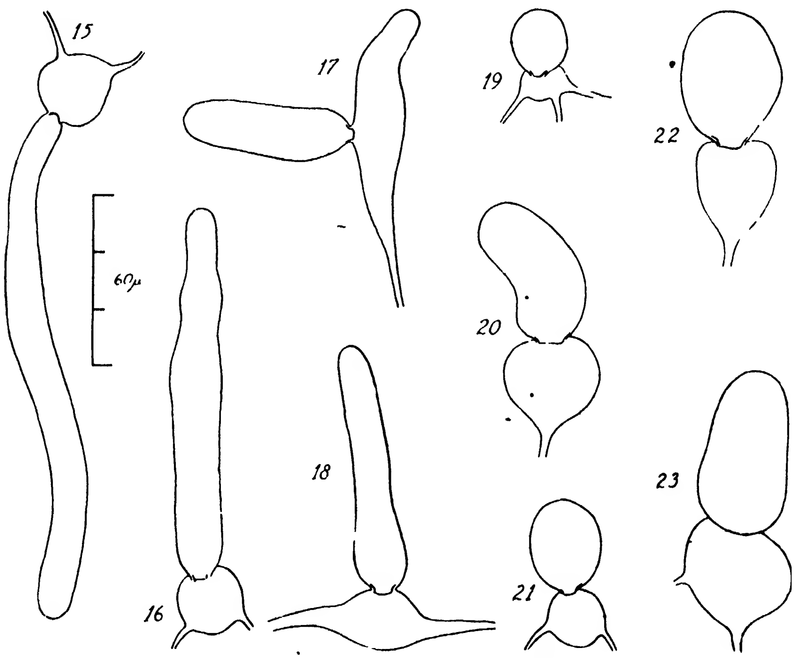
It is concluded from the information obtained in this study that *P. Euglenae*, as the binomial commonly heretofore has been used, represents two genetic entities whose thalli can be distinguished in either the vegetative or the zygospore stage. It is further concluded that the fungus grown in cultures A, C and DM is identical with Nowakowski's *P. Euglenae* var. *minor*. While admittedly our knowledge of genetic relationships as applied to taxonomy in this group of the fungi is extremely meager, it appears that most students prefer to look upon comparable characters in other genera as of specific rank. *Phlyctidium spinulosum* (Sparrow, **1933**), *Phlyctochytrium chaetiferum* (Karling, **1937**), species of *Micromyces*, *Micromycopsis* and others are differentiated wholly or in part on the possession of thallus, sporangial or resting spore ornamentation. The validity of this practice is unquestioned in most instances, and the use of definite ornamentation as a diagnostic character has almost come to be taken as a matter of course. However, recent cultural studies by Shanor (**1939a**, **39b**) and McLarty (**1939**; **41**) seem to indicate that spines, fibrillae, warts and other types of projections are not, in themselves, diagnostic but may be so when they appear regularly at a given stage in the life history through successive generations.

In consideration of the persistence in culture of the distinctive features of these two fungi, it is the opinion of the writer that *P. Euglenae* var. *minor* is to be considered a species separate and distinct from *P. Euglenae*. It is suggested that the latter name be reserved for those thalli whose zygospores are spiny-walled and which agree in other characters with those tabulated and described for this form; *P. laevis* is proposed as the species name for the smooth-walled form.

POLYPHAGUS EUGLENAE Nowakowski sense nov.

Syn. *P. Euglenae* Nowakowski pr. p. (see Sparrow, **1943**, p. 299).

Prosporangia extramatrical, lying free in the medium, rarely sessile, typically fusiform, clavate, commonly spherical, ellipsoid, elongated or irregular, 7.2–38.4, av. 18.1 μ in diameter × 12.2–200.0 or more, av. 36.2 μ long; with 2–8 rhizoidal axes about 6 μ in diameter at their point of origin, the latter branched and rebranched with their tips imbedded in a number of hosts. Zoospo-



FIGS. 15–18. *Polyphagus Euglenae;* 19–23, *P. Laevis.*

rangia typically lateral on a fusiform prosporangium, usually elongated, tubular and tapering toward the apex, occasionally short-cylindrical or curved, rarely ovoid or ellipsoid, 7.6–36.0, averaging 18.7 μ in diameter × 21.8–179.2 or more, av. 107.7 μ long, with thin smooth wall, opening by an apical deliquescence pore, containing one to many hundreds of zoospores. Zoospores cylindrical to ellipsoid, 3–5 μ in diameter × 6–13 μ long, containing a single posteriorly located pale yellow oil droplet and provided with a long posterior flagellum, escaping individually and generally swimming

away immediately, positively phototactic, occasionally some zoospores germinating inside the sporangium. Antheridia fusiform, clavate, spheroid or irregular, 4.1–14.2, av. 9.4 μ in diameter × 6.6–35.4, av. 16.7 μ long; oogonia fusiform, saccular or irregular, 12.3–21.4, av. 16.3 μ in diameter × 14.8–61.7, av. 26.3 μ long. Zygospore spheroid, ovoid or wide-fusiform, 10.6–26.3, av. 17.9 μ in diameter × 18.0–27.0, av. 22.6 μ long, with a thick, 2-layered wall, the exospore bright yellow to amber or brown and beset with delicate conical spines or rarely with bullations, endospore smooth and hyaline; subterminal on an elongated conjugation tube 6.5–67.2, av. 18 μ long × 1.8 μ in diameter, separated from oogonium by a portion of that tube 4.9–13.2, av. 8.9 μ long × 3.3 μ in diameter; functioning in germination as a prosporangium.

Parasitic on the cysts of various species of *Euglena,* especially *E. viridis* and *E. sanguinia,* and on cysts of *Chlamydomonas Reinhardi* and *C.* sp.; apparently of general occurrence in the northern hemisphere.

Polyphagus laevis (Nowakowski) comb. nov.

Syn. *P. Euglenae* Nowakowski pr. p. (see Sparrow, **1943**, p. 299, 300).

P. Euglenae var. *minor* Nowakowski (see Sparrow, **1943**, p. 300).

Prosporangia extramatrical, lying free in the medium, rarely sessile, typically globose, 12.3–28.4, av. 22.4 μ in diameter, or ovoid, 11.2–26.2, av. 19.2 μ in diameter × 18.4–28.6, av. 24.0 μ long, occasionally irregular in shape, with 1–6 rhizoidal axes about 3 μ in diameter at their point of origin, the latter extensive, branched repeatedly and with their tips imbedded in a number of hosts. Zoosporangium located at any point on surface of prosporangium but typically diametrically opposite the insertion point of the most prominent rhizoidal axis, typically ovoid, 19.2–35.2, av. 27.5 μ in diameter × 25.6–41.6, av. 36.5 μ long, with thin smooth wall, opening by an apical or subapical deliquescence pore, containing several to many zoospores. Zoospores ovoid to elongated, 3.0–3.4, av. 3.3 μ in diameter × 5.0–6.5, av. 6.4 μ long, containing a single posteriorly located, pale bluish-green droplet and provided with a long posterior flagellum, escaping individually and generally swimming away immediately, positively phototactic, rarely germinating inside the sporangium. Antheridia spherical, ovoid or irregular, 4.2–15.4, av. 9.8 μ in diameter × 6.4–23.8, av. 16.5 μ long; oogonia spherical, ovoid or irregular, 14.0–28.2, av. 18.0 μ in diameter ×

15.4–25.2, av. 20.8 μ in diameter. Zygospores ovoid, truncated, spheroid, elongated, reniform, lacrymoid, clavate, constricted, or irregular, 14.0–28.2, av. 19.7 μ in diameter × 19.6–35.0, av. 26.2 μ long, with thick, 2-layered wall, the exospore smooth, hyaline, rarely pale yellow, the endospore smooth and hyaline, terminal on a more or less elongated conjugation tube, 2.8–77.0, av. 28.2 μ long × 1.4–5.2, av. 3.0 μ in diameter and sessile on the larger gametic thallus, functioning in germination as a prosporangium.

Parasitic on the cysts of *Euglena viridis, E.* sp. and on the cysts of *Chlamydomonas* sp.; apparently of general occurrence in the northern hemisphere.

SUMMARY

This study is concerned with clarification of a controversy concerning the relationship and taxonomy of smooth zygospore and spiny zygospore-producing races of *Polyphagus Euglenae* which occur primarily as parasites on various species of *Euglena*.

Thalli from four collections were cultivated in liquid and on agar by supplying them with living *Euglena* cysts. Zygospores formed in cultures from two collections were smooth-walled and sessile on the oogonium while zygospores from one collection were spiny-walled and attached to the oogonium by a tube. Zygospores of both kinds were formed by thalli cultivated from a fourth collection. Unifungal cultures were prepared for the mono-zygosporic collections, and the two zygosporic races of the remaining collection were isolated in unifungal cultures.

The zygosporic character of each isolate remained constant during subsequent cultivation.

The spiny form is identical in part with *P. Euglenae* as originally described; a revised diagnosis is given for it. The smooth form is identical with *P. Euglenae* var. *minor;* it is rediagnosed and raised to specific rank as *P. laevis*.

The process of conjugation is fundamentally similar in both species; this is in confirmation of Nowakowski's observations.

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UNIVERSITY OF WISCONSIN IN MILWAUKEE,
MILWAUKEE, WISCONSIN

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EXPLANATION OF FIGURES

All figures were drawn from living material with the aid of an Abbe camera lucida, using a 10 × ocular and a 4 mm. objective; original magnification of figures 1–14 is 1500 × following enlargement by means of a pantograph, and original magnification of figures 15–23 is 750 ×.

FIGS. 1–8. *Polyphagus laevis*. 1–2, typical proportional relationship of zygospore to antheridium and oogonium; 3, zygospore with atypically dense contents; 4, zygospore with gametangia of approximately equal size, the antheridium provided with a tube; 5, zygospore with antheridium attached by an abnormally short tube; 6, zygospore with attached sessile gametangia, a and b, whose sexual nature is not apparent; c, immature thallus merely growing in the vicinity; 7, oogonium to which two zygospores and their connected antheridia are attached; 8, antheridium that has conjugated with two oogonia resulting in the formation of a zygospore at a and at b.

FIGS. 9–14. *P. Euglenae*. 9, typical zygospore connected to fusiform antheridium by an elongated tube; parasitized *Euglena* cells at a and b; 10, zygospore connected laterally to fusiform oogonium and apically to a clavate antheridium; 11, zygospore beset with delicate scattered bullations; mass of granules at a represents the remains of two *Euglena* cysts; 12, appearance of typical zygospore, oogonium and antheridium, the former with more delicate spines at the two ends; 13, zygospore with uniformly distributed spines of equal size; 14, zygospore with widely scattered spines of uniform size.

FIGS. 15–18. *P. Euglenae*, sporangia and prosporangia.

FIGS. 19–23. *P. laevis*, sporangia and prosporangia.

SPECIES OF SYNCHYTRIUM IN LOUISIANA
II. SPECIES OF LOUISIANA SYNCHYTRIUM

MELVILLE T. COOK

(WITH 1 FIGURE)

This is a record of five species of *Synchytrium* found in the vicinity of Baton Rouge, Louisiana, between January 4 and April 12, 1945. Three of them appear to have been previously undescribed. The descriptions in this paper are based on fresh material.

Synchytrium Erigerontis sp. nov.

This species attacks the epidermal cells in basal leaves of *Erigeron philadelphicus* L. causing them to turn yellow. The galls start as very small green papillae visible on either surface but rarely visible on both. A few were found on the stems. They are more abundant on the margins than on other parts of the leaves, and turn black with age. There is no evidence of a gall until the fungus is about half its full size. The fungus may be entirely submerged in the tissues of the host plant except for the opening to the surface, but in most cases one-half is submerged in the tissue of the leaf and the other half in the gall, which projects above the surface. No true galls are formed in the former type of infection, but the enlarged infected cells frequently extend from epidermis to epidermis. The opening leading to the infected cell is always visible if the sections are cut properly. The leaf may be slightly thickened or about twice as thick as normal. The host cells around the infected cells are not modified but are replaced by the enlarged, infected cells. When the infected cell is ready for segmentation it measures 126–167 μ. The fungus is yellow, becoming orange-colored, 45–160 μ in diameter; when mature it is surrounded by a thick, yellow wall consisting of three layers. The

inner layer is almost hyaline. The middle layer is thick and so brittle as to break readily, but becomes thin at maturity. The disintegrating contents of the host cell is yellow or black and 5–15 μ in thickness but the host nucleus is rarely seen. When two sori occupy the same cell they are hemispherical in form.

Gallis parvis, colore a viridi usque ad nigrum differentibus in utraque superficie marginum foliorum basalium depressis aut semi-depressis in folium, 126–167 μ in diametro. Soris colore a flavo usque ad aurantium differentibus, 45–160 μ in diametro.

Hab. *Erigeron philadelphicus* L.

Synchytrium Stachydis sp. nov.

This species attacks the epidermal cells and causes galls of various sizes, usually on the upper surfaces of the leaves and on the petioles and stems, and occasionally on the lower surfaces of the leaves of *Stachys agraria* Cham. & Schlecht. The epidermal cells surrounding the infected cells grow and cause galls composed of two or more layers of large, thin-walled cells. In many cases the epidermal cells of the galls become infected and large compound galls are formed. The thickening of the leaves causes the galls to be about one-half submerged. The galls are large, compound, and usually the result of infection of the epidermal cells of the galls by the fungus. They are variable in form; the single galls are almost spherical and on short pedestals which are cylindrical or almost columnar but slightly constricted at the base. This character is usually lost in compound galls. The galls are green, sometimes light green, becoming brown. The galls may start to form very soon after infection of the epidermal cells or may be delayed until the fungus is about one-half full size. The infected cell is surrounded by the growth of the host tissues until about half grown; at that time the gall begins to form. There is little or no distortion of host tissues within the leaf. The galls are usually crowded into a mass and cause thickenings of the leaves. The infected cells are never completely covered by the growth of the surrounding cells, but some have a much larger aperture than others. The aperture always enlarges with maturity. Simple galls measure 100–200 μ, compound galls 220 μ or more. They are composed of parenchyma cells.

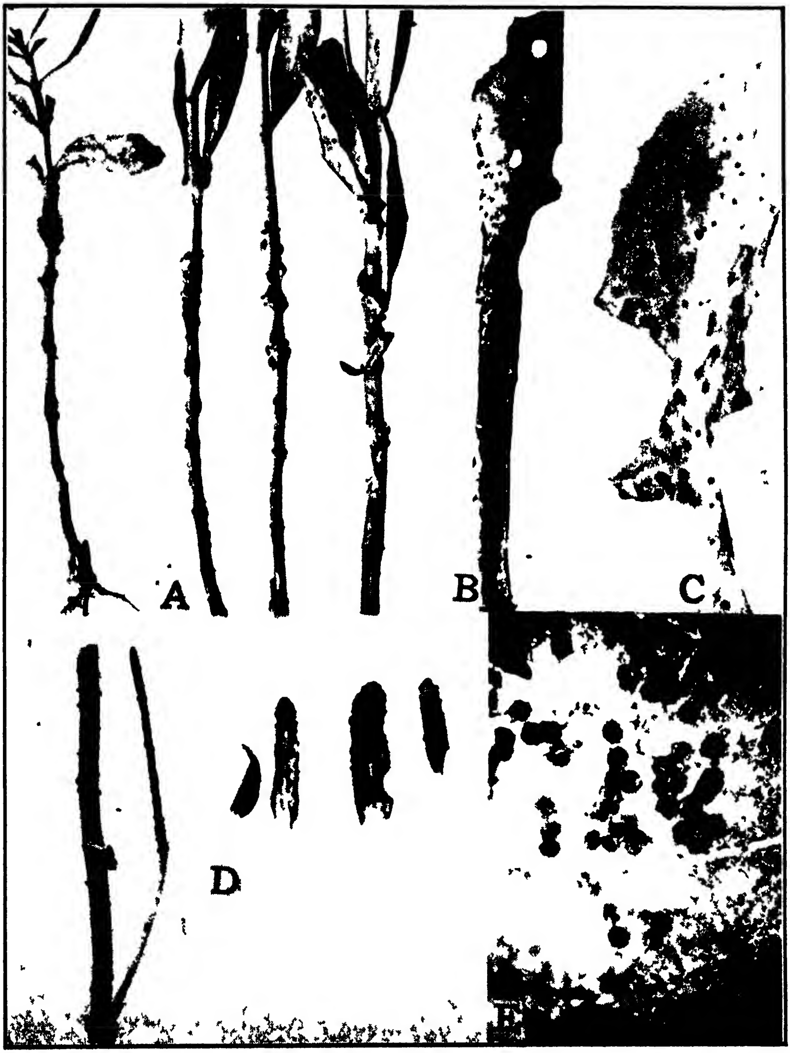


FIG. 1. A, *Synchytrium Lythri*, B, *S. Erigerontis*, C, *S. aureum*, D, *S. globosum*, E, *S. Stachydis*.

The fungus is yellow, measuring about 60–70 μ, but does not completely fill the infected cell and only a small amount of the host cell material persists. The wall around the fungus forms early, consists of two layers, is thick and hard (but the space between the fungus and the wall of the host cell is usually clear). Two or three fungi may be found in the same cell but are not necessarily the same age, judging by development. The development and formation of sporangia is in the usual manner. Young and old galls may be very close together in a leaf, indicating that the fungus may infect cells of various ages.

Gallis simplicibus et globosis aut compositis, viridibus maximam partem in superficiebus superioribus foliorum, petiolorum et stirpium. Galli simplices nonnonquam in stylobatibus siti, 100–200 μ, soris flavis 60–70 μ.

Hab. *Stachys agraria* Cham. & Schlecht.

Synchytrium Lythri sp. nov.

Hemispherical or oblong galls, numerous, sometimes compound, variable in size, mostly on basal parts of stems, and on leaves and petioles of *Lythrum alatum* Pursh. and measure about 80–100 μ. Leaves frequently thickened. The infected cell is spherical with long neck. The infections are always epidermal but in advanced stages frequently have the appearance of being sub-epidermal. Fungus is yellow and measures about 30–40 μ at maturity. The wall around the fungus is composed of three layers.

Gallis oblongis aut semiglobosis plerumque simplicibus in stirpibus, foliis petiolisque sitis, colore a viridi usque ad subrufum differentibus, 80–100 μ, soris flavis, 30–40 μ.

Hab. *Lythyrum alatum* Pursh.

SYNCHYTRIUM AUREUM Schroeter on *Lactuca* sp.

This species causes leaf galls which are usually concave on the lower side of the leaf and convex on the upper side but sometimes the reverse. Most infections are in epidermal cells on the lower surface but the galls are usually formed on lower, regardless of point of infection. This is different from the galls caused by most species of *Synchytrium*, which cause galls on the same surface as the infected cells. Galls usually start soon after infection but there are variations as to time. A small papilla develops in the center

of the concave side, which is usually on the lower surface. The leaves may be slightly thickened at point of infection without gall formation. The galls are small and green at first but become large with age and the papillae becomes black and about 60–90 μ when mature. The fungus is yellow and 20–30 μ when mature.

This species has been reported from several countries and on nearly 200 species of host plants. In all probability many of these records are incorrect.

SYNCHYTRIUM GLOBOSUM Schroeter.

This species causes small, green pustules on either side of leaves and on stems of *Veronica perigrina* L. They become brown and finally black and measure about 60–80 μ. The infected cells become pear shaped and the basal halves of those on the leaves are submerged in the host tissues while only a very small part of those on the stems are submerged in the cortex. The galls are more or less conical and composed of very large parenchyma cells. The infected cells on the upper surface are usually about half embedded in palisade tissue while those on the lower surface are usually completely embedded in the mesophyll. The fungus is yellow and about 35–40 μ in diameter.

This species is found in northern European countries and in Iceland. It was described in 1870 and has been reported as attacking about twenty species of host plants. The species in Louisiana occurs on an entirely different species of *Veronica* from any previously reported, is only about half the size of the European species and differs in some other details.

The author wishes to express his thanks to the workers mentioned in the first paper and to Dr. Illo Hein for material and other assistance in the work.

DEPARTMENT OF BOTANY AND PLANT PATHOLOGY,
LOUISIANA STATE UNIVERSITY,
BATON ROUGE, LOUISIANA

EXPLANATION OF FIGURES

FIG. 1. A. *Synchytrium Lythri,* natural size. B. *Synchytrium Erigerontis,* natural size. C. *Synchytrium aureum,* natural size. D. *Synchytrium globosum,* natural size. E. *Synchytrium Stachydis,* enlarged.

PERICONIA BLIGHT OF HEVEA

John A. Stevenson and Ernest P. Imle

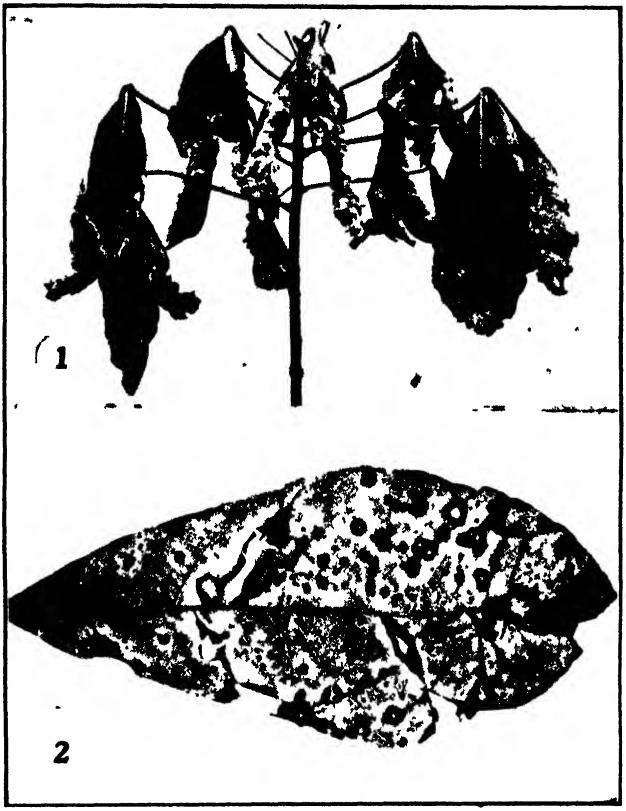
(with 4 figures)

In December, 1943, an unknown disease characterized by a severe leaf spotting was found in a nursery of *Hevea Spruceana* at Turrialba, Costa Rica. Six weeks later, following a prolonged rainy period, this disease had reached epiphytotic proportions in the spruceana nursery where it was causing leaf, petiole, and twig blight, and also was producing minor damage in a nearby nursery of *Hevea brasiliensis* seedlings. In addition to Turrialba (elevation 2000 ft.) the disease was noted near Gualipes, Costa Rica (elevation 600 ft.). An earlier observation of the same disease was made by W. J. Martin on *H. brasiliensis* at El Palmar, Tezonapa, Mexico, but no collections were made.

The leaf spots are circular to oval, at times somewhat irregular or elongated along the veins, but not vein limited, appearing much the same on both surfaces. Primary lesions vary in diameter from two to ten millimeters, but frequently coalesce, particularly on younger leaves, to involve an entire leaf and may bring about premature abscission. The spots are brown at first, becoming ashen at the center with a brown border, and on mature leaves (fig. 1) they are often ringed by a chlorotic halo. Necrotic areas split irregularly and may even fall away in part. Petiole lesions are common and, when severe, cause leaf abrasions or petiole breakage. Petiole lesions or leaf spots sometimes spread down to the leaf axils and cause sunken twig cankers or die-back of young soft twigs (fig. 2).

This disease has been found on *Hevea brasiliensis*, *H. Spruceana*, *H. guianensis*, *H. Benthamiana*, and on hybrids of *H. brasiliensis* × *Spruceana*. *H. Spruceana* clones selected for resistance to South American leaf blight (*Dothidella Ulei* P. Henn.) are readily attacked. *H. brasiliensis* clones, highly resistant to *D. Ulei*, have been heavily infected when growing under a thin overstory of

heavily infected *H. Spruceana* plants, but these same clones showed almost no damage when grown 20 to 30 feet away from the heavy source of inoculum and out in full light. The following *Dothidella*-resistant *brasiliensis* clones have been damaged, some



FIGS. 1, 2 *Perconia*, blight of *Hevea*.

severely, under the above described conditions: F–409, F–211, F–1620, FB–45, FB–54, FB–79, FB–3363, and FB–3384. F–409 was least damaged.

The disease is very destructive on *H. Spruceana* during prolonged periods of rainy weather, but all evidence at hand indicates that it will not become a problem on the important rubber-producing species of commerce, *H. brasiliensis*, except where this species is grown in a mixture with the highly susceptible *H. Spruceana*.

This combination of species will be used in Latin America only in a few isolated gardens for production of hybrid seed, and artificial means of control could be used in such small areas should the disease become threatening.

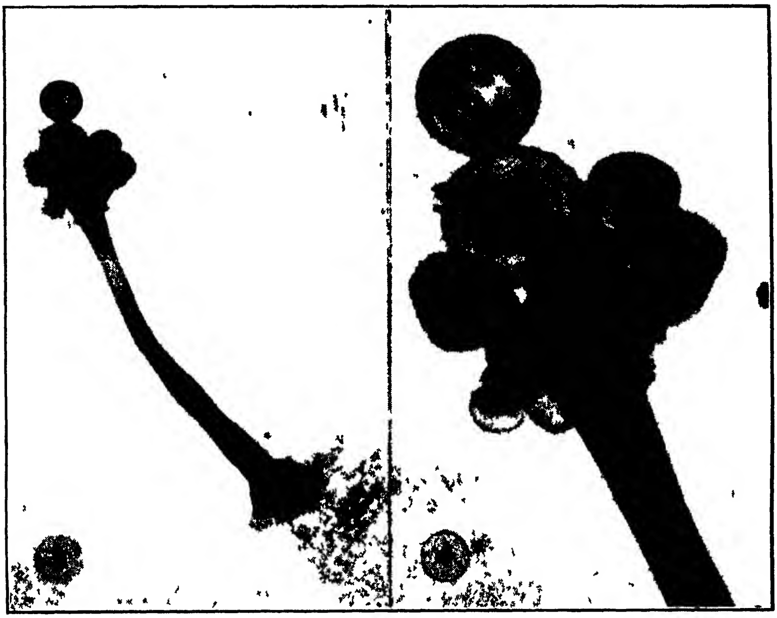
Numerous lesions were produced on leaves and petioles of *H. Spruceana* seedlings without wounding when infected leaves which were sporulating were suspended above young flushes during rainy weather. Infection was also obtained when conidia from diseased leaves were atomized onto wounded and non-wounded three-quarter grown leaves of clone F–6398 (a hybrid of *H. brasiliensis* and *H. Spruceana*). Visible lesions were noted 7 days after inoculation and conidia were produced within 10 days. The pathogen grows and sporulates readily on potato dextrose agar.

The relatively small number of conidia produced per lesion and their large size as described hereafter probably account to an appreciable extent for the slow spread of the disease. Susceptible plants growing beneath a heavy source of inoculum have become seriously diseased in two weeks, while similar plants 300 yards away remained disease free for 3 months or until inoculum was introduced artificially. The disease, though very destructive during prolonged periods of rainy, cloudy weather, is reduced almost to the point of disappearance during the dry season. Viable conidia have been obtained from leaf spots on old leaves infected 5 months earlier, indicating that the pathogen may survive a considerable period of unfavorable weather and initiate new infections when the rains begin again.

A species of *Periconia* has been found constantly associated with diseased areas, which is characterized by relatively large black erect conidiophores bearing terminal clusters of globose conidia (FIGS. 3 and 4). The conidiophores are scattered individually over the lesions and appear on both leaf surfaces. They are readily found with a hand lens and can even be noted without the assistance of this instrument when an infected leaf is held against the light. A *Phyllosticta* is sparingly present on some infected leaves, but appears to be entirely secondary.

Previous reports of the occurrence of *Periconia* on *Hevea* are few. Petch (The Physiology and Diseases of *Hevea brasiliensis*, p. 262. 1911) notes the occurrence of *P. pycnospora* Fres. as a

saprophyte on diseased leaves in Ceylon. This species has conidia only 12–17 μ in diameter and in this and other morphological characters differs markedly from the Costa Rican fungus under discussion. *P. pycnospora* is generally distributed as a saprophyte on stems, leaves, and other plant parts of a very wide range of phanerogamic substrata and cannot be confused with our species



FIGS 3, 4. *Periconia,* blight of *Hevea*

Weir (A pathological survey of the Para rubber tree in the Amazon Valley. U. S. D. A. Bull. 1380, p 88 1926) reports the presence of *Periconia byssoides* Pers. on leaves of *H. brasiliensis* associated with *Gloeosporium* and other leaf fungi in the Amazon region of Brazil. Specimens to check this report have not been found. *P. byssoides* is a rather vague species which Saccardo says is not sufficiently distinct from *P. pycnospora.* The name has been used by many workers for a fungus of similar habits to *P. pycnospora,* with which as already indicated it is probably synonymous.

Very few species of *Periconia* have been reported as plant parasites and of these none have been heretofore known on members

of the Euphorbiaceae. The several species described as parasitic on leaves or other plant parts all differ from the *Hevea* species in having much smaller conidia and in other specific morphological characters. Similarly the more numerous saprophytic species all differ along the same lines. The species on *Hevea* is therefore described as new.

Periconia Heveae sp. nov.

Spots amphigenous, circular to irregular, 2–12 mm. in diameter, brown at first, then with ashen gray centers, and deep-brown, definite borders, 1–3 mm. across, not raised; *vegetative mycelium* scanty, intramatrical, light-brown, septate, branching, 3–4 μ in diameter; *conidiophores* numerous, amphigenous, scattered, erect, rigid, unbranched, dark-brown microscopically, black shining macroscopically, without stromatic base, 2- rarely 3-septate, 250–400 μ long (average about 300 μ), with bulbous basal cell 45–90 μ long, 24–30 μ in diameter at base, 15–18 μ in diameter above; *apical cell* short clavate, slightly constricted at septum, light-brown, 30–45 × 20–25 μ; *sporogenous cells* in a whorl at base of apical cell, minutely verruculose, 10–15 × 18–24 μ; *conidia* globose, deep brown, strongly verrucose, 25–45 μ in diameter (usually 30–35 μ), short catenulate, terminal conidium only reaching extreme size.

On living leaflets, petioles, and smaller twigs of *Hevea Spruceana* (Benth.) Muell. Arg. (Euphorbiaceae), Turrialba, Costa Rica, Ernest P. Imle, Feb. 5, 1945 (Type, Mycological Collections, Bureau of Plant Industry, Beltsville, Md. 71424); *Hevea brasiliensis* (H.B.K.) Muell. Arg., Turrialba, Costa Rica, Ernest P. Imle, Feb. 5, 1945, Myc. Coll. 71425. Portions of the type collection have been deposited in the herbaria of the Dept. of Plant Pathology of Cornell Univ., the Farlow Herbarium, the New York Botanical Garden, the University of Michigan, and the Imperial Mycological Institute, Kew.

Maculis amphigenis, orbiculatis vel irregularibus, definitis, cinereis, marginibus atro-brunneis, 2–12 mm. diam.; *conidiophoris* amphigenis, rigidulis, multis, erectis, disseminatis, usque 400 μ longis, 15–18 μ diam., 1–2 septatis, nigris, sub microscopio atro-brunneis, ad basin abrupte bulbosis inflatis; *cella terminali* clavata, ad septum leniter constricta, sub brunnea, 30–45 × 20–25 μ; *cellulis sporogenis* verticillatim ad basin cellae terminalis dispositis, concoloribus ellipticis vel ovalibus, verruculosis, 30–45 × 20–25 μ; *conidiis* globosis, dense verrucosis, brunneis, breve et fugaciter catenulatis, 25–45 μ diam.

BUREAU OF PLANT INDUSTRY STATION,
BELTSVILLE, MD., AND
U. S. D. A. RUBBER STATION,
TURRIALBA, COSTA RICA

EXPLANATION OF FIGURES

FIGS. 1–2. *Periconia Heveae* on *Hevea Spruceana.* Fig. 1, terminal twig showing blighting effect previous to premature abscission; Fig. 2, an infected leaflet.

FIGS. 3–4. *Periconia Heveae.* Fig. 3, conidiophore × 150; Fig. 4, terminal portion of conidiophore × 430. The apparent terminal conidium has floated in and lodged against the larger and true terminal conidium.

CONIDIUM FORMATION IN SPECIES OF ASPERGILLI

Gladys E. Baker

(with 64 figures)

Relatively little attention has been devoted within recent years to details attending the development of condiophores and conidia in the *Aspergilli*. The genus early drew attention but the first publications need both confirming and amplifying. De Bary's papers on *Aspergillus glaucus* and *Eurotium* (**1854**; **1870**) included no cytological details; Dangeard (**1907**) figured nuclei in cells of some species, but his observations were far from complete for any species. More thorough cytological observations were made by Fraser and Chambers (**1907**) and Dale (**1909**). The most detailed report of nuclei is Wakyama's investigation (**1931**) of chromosome numbers in several species of *Aspergilli.*

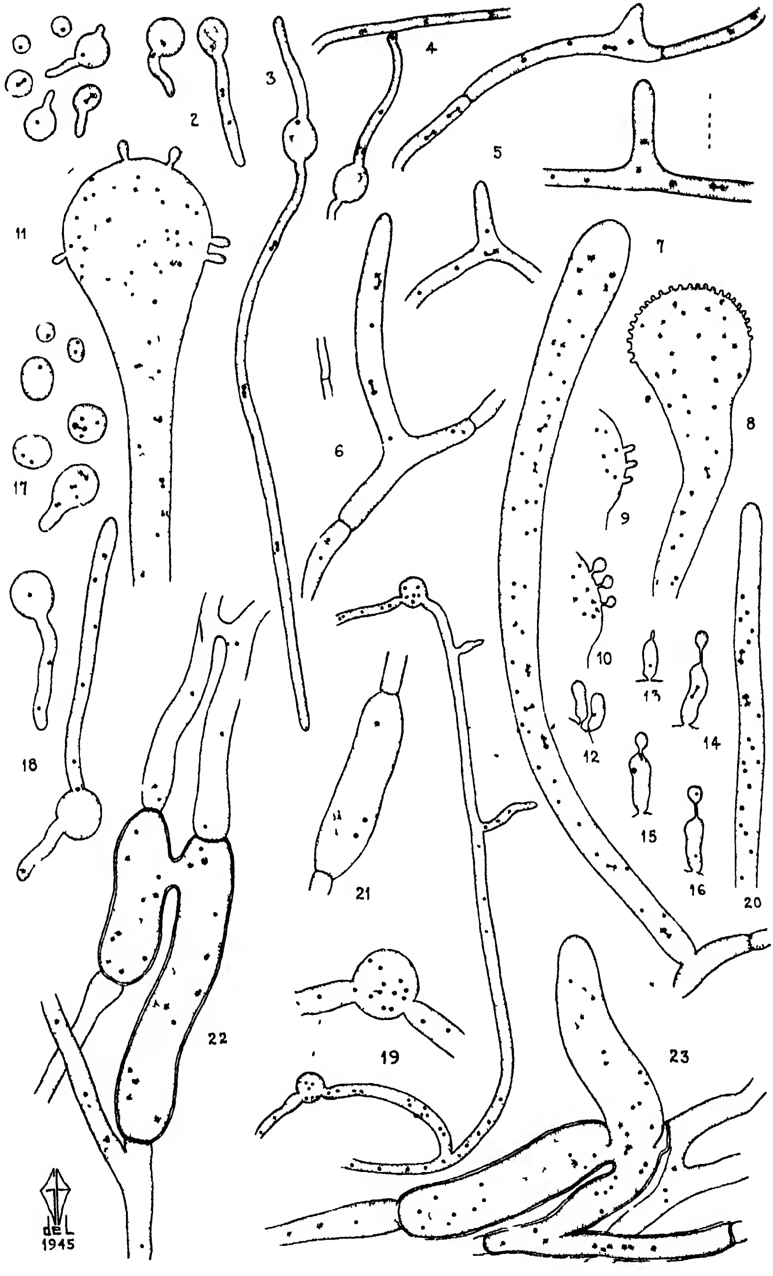
Because of interest in the problem of heterokaryosis and variation in imperfect fungi it seemed important to investigate not only the nuclear condition of *Aspergillus* conidia but also their subsequent stages of development. Even though there is little critical reference material on the subject, the publications describe two types of behavior in conidial development. Dangeard, for example, clearly states (l.c.) for two species, *A. flavus* and *A. fumigatus,* that the conidia are uninucleate. Moreover, he segregated *A. glaucus* as *Eurotium herbariorum,* giving it generic distinction because the conidia were multinucleate. Fraser and Chambers (l.c.) and Dale (l.c.) reported that the species which they investigated, *A. herbariorum* and *A. repens,* had multinucleate conidia at maturity. Thom and Church (**1926**) discuss the occurrence of uninucleate conidia in several other species of *Aspergillus* observed by themselves or others. In addition they refer to Dangeard's multinucleate series (the *A. glaucus* group) and suggest that if this condition obtains for the entire *glaucus* group that it

then forms a distinct line in the entire series of *Aspergilli*. But these observations are not supported beyond their statement.

In this investigation four species of *Aspergilli* have been employed: *A. echinulatus* (Delacr.) Thom & Church (N. R. R. L. strain no. 131); *A. repens* (Cda.) De Bary (N. R. R. L. strain no. 17), both of the *A. glaucus* series as defined by Thom and Raper (**1941**); and two antibiotic producing species, *A. clavatus* Desm. and *A. fumigatus* Fres., both from the laboratories of Dr. S. A. Waksman. The methods of study were the same as those used in an investigation of *Penicillium notatum* (Baker, **1944**), supplemented by sections cut in paraffin at 3, 5, and 7 μ. By the latter method mature conidiophore stages which are mostly too large for the agar-film method could be handled to better advantage. All slides were stained by Heidenhain's iron-alum haematoxylin schedule.

Morphologically *A. clavatus* and *A. fumigatus* differ in conidiophore origin as the former possesses a foot-cell which the latter lacks. Cytologically there is little difference in the details of their conidial formation. In fact their nuclear cycles offer no critical differences as far as possible nuclear distribution and heterokaryosis are concerned.

When first formed a conidium of *A. fumigatus* is uninucleate. At germination the conidia may still be uninucleate or they may have become binucleate through a single mitotic division. Uninucleate, ungerminated conidia usually are much smaller in diameter than the germinating conidia, hence are readily distinguished. At germination a single germ tube emerges though occasionally a second one is formed almost as soon as the first one (FIG. 1). By the time the germ tube is of a conspicuous length the cell is binucleate usually. One nucleus migrates into the elongating tube, there to divide further, and the other remains in the body of the conidium proper (FIG. 2), moving out into the second germ tube later. Usually the formation of the second germ tube is delayed until two or more nuclear divisions have taken place in the first germ tube (FIG. 3). The nucleus which was left in the conidium does not divide until it moves into the second germ tube. Often the second of the germ tubes is shorter and it soon anastomoses with the longer, first formed hyphal out-



FIGS. 1–23.

growths of other conidia (FIG. 4). Anastomoses are frequent at the 25 hour growth level, but are neither so abundant nor striking as those seen in *Penicillium notatum*. The mycelium in its early stages is non-septate. Much later septa may appear forming cells with one or more nuclei. In active stages of growth the nuclei divide freely in the mycelium (FIG. 5).

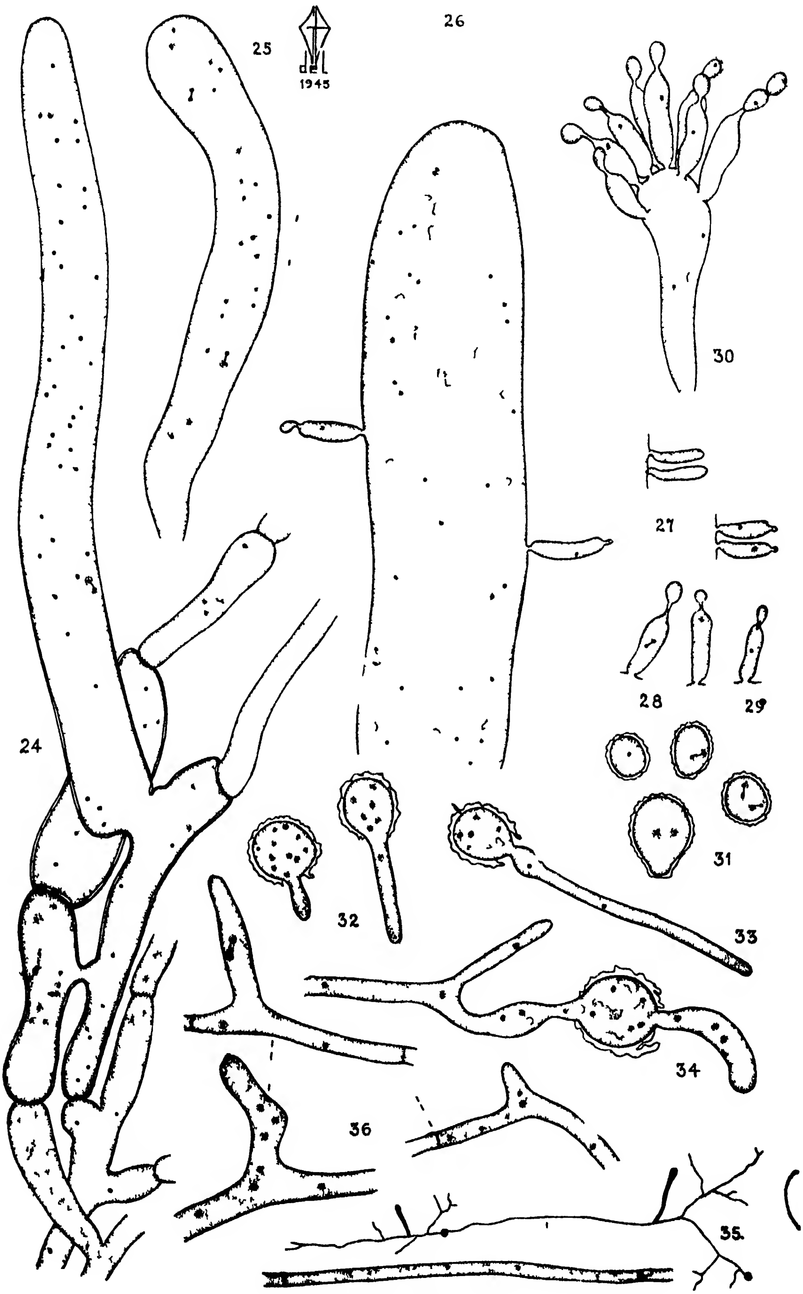
Slide cultures about 40 hours old show a good distribution of conidiophores in varying stages of development. A pair of septa in a hyphal strand ultimately delimits the plurinucleate initial cell of the conidiophore. As the mycelial strand from which a conidiophore arises is multinucleate following anastomoses, the nuclear distribution in the region of the conidiophore initial is not necessarily identical. The initial cell puts out a branch at right angles to the main hypha which enlarges into the conidiophore. It appears that this branch receives one nucleus followed by several others; the nuclei sometimes are already in division as they move into the elongating conidiophore. However, since no septum separates the two parts of the conidiophore there seems to be no way of knowing whether the several nuclei in a young conidiophore originated from one or more nuclei. The nuclei divide actively as the conidiophore elongates and increases its diameter in the distal portion. Incipient phases of the conidiophores are easily recognized because the cytoplasm is densely aggregated even before the septa form; in addition the diameter of both the initial cell and the budding portion is considerably in excess of the diameters of the adjacent assimilative hyphae (FIGS. 5, 6). Conidiophores may also arise directly from a conidium or from the products of several fused conidia.

Developing conidiophores are densely filled with cytoplasm accompanied by many actively dividing nuclei. At maturity the apex expands into the large flask-shaped vesicle, also multinucleate, and the stalk and basal portions become more or less vacuolated. A few scattered nuclei remain in the stalk (FIG. 7). Phialides develop simultaneously as budding protuberances over the entire upper vesicle surface (FIGS. 8–11). Each phialide is in open communication basally with the vesicle at all times. One nucleus moves into each phialide when it is nearing its full size (FIG. 12). When a phialide is mature a fine projection appears

apically which enlarges into the first conidium. Conidium and phialide remain in connection by means of a narrow canal-like tube. The nucleus of the phialide divides once while the conidium is forming and one of the daughter nuclei moves through the canal into the spore, attenuating as it passes through the narrow connective (FIGS. 13–16). All the nuclei of the conidiophore do not enter conidia; some remain in the vesicle and the stalk, the latter by this time is usually quite vacuolate. Successive conidia appear to be formed acropetally in similar fashion.

For *Aspergillus clavatus* the process of phialide and conidium formation on the vesicle is identical with that of *A. fumigatus*. Every phialide has a single nucleus and it produces a series of uninucleate conidia. Successive stages of development of these two species differ in the details of the stages between conidial generations, although essentially the processes involved are the same in that they both allow for the possibility of free nuclear interchange before the next generation of conidiophores produces conidia.

When a group of conidia is inoculated onto the surface of an agar film on a slide, the nucleus of the conidium undergoes several divisions within the first 12 hours, so that the spore may contain anywhere from two to six nuclei before the emergence of a germ tube can be detected (FIG. 17). Typically one nucleus remains in the body of the spore, and the rest continue to move out into the elongating hyphae and divide there (FIG. 18). Anastomoses are common after 21 hours. By then a second germ tube has appeared and soon enters into anastomosis with another hyphal strand (FIG. 19). The original conidia are often still strikingly multinucleate at this stage. As the hyphae grow in a radial pattern from the focus of the inoculum, the aseptate mycelium branches freely and it contains many nuclei well distributed throughout the strands, with the exception of the growing apices themselves (FIG. 20). Later, after 40 hours growth, more fusions occur between hyphae. As portions of the mycelium become septate and much enlarged they form the initials of the foot-cells preliminary to conidiophore production (FIGS. 21–24). The interrelations of these fusing cells is often complex and can be followed best on agar-film slides, since they usually do not lie in a common plane. Foot-cell initials stand out clearly in such preparations by



FIGS. 24–36

virtue of their denser cytoplasm and heavy walls. These initials have more than one nucleus and by mitotic divisions soon increase the original number markedly. Foot-cells may occur in clusters following anastomosis, but a single group of cells segmented from the hyphal strand gives rise to one conidiophore by budding and subsequent elongation. From the beginning the conidiophore is multinucleate, the number of nuclei increasing enormously up to the time of vesicle formation (FIGS. 25, 26). As in the preceding species, conidiophores occasionally are direct products of conidial germination, or arise from close interconidial fusions. Each conidiophore expands to a clavate vesicular apex from which the phialides are produced simultaneously. At maturity each phialide then buds out a succession of uninucleate conidia (FIGS. 27–30).

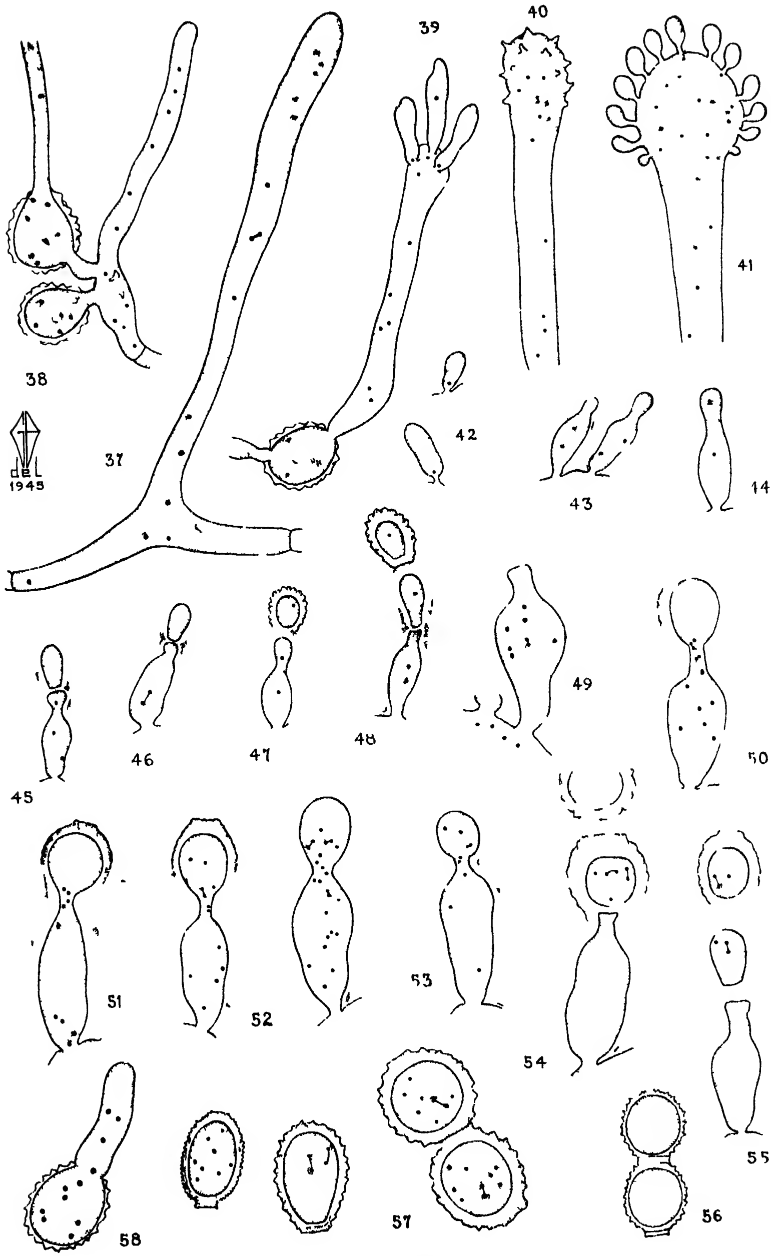
Aspergillus repens and *A. echinulatus* are species without foot-cells belonging to the *A. glaucus* group. The species included in that group have in common, according to Thom and Raper (l.c.), the production of conidial heads borne on septate stalks and perithecia of homothallic origin (the latter character holds for all but one species). Of those producing perithecia further subdivision is made on the basis of ascospore size, large or small. *A. repens* belongs with the small-spored forms. Its conidia vary considerably in size as they increase greatly between the time of their formation and germination. Spores removed from the surface of a culture into a drop of nutrient medium on the surface of a slide spread with Mayer's adhesive and allowed to come just to the drying point before killing and fixing in Bouin's fixative, will show a range from formation size to germination size with their attending nuclear conditions (FIG. 31). Newly formed conidia are uninucleate. Nuclear divisions and increase of spore size are concomitant until at germination the conidia are multinucleate (FIG. 32). Next a single germ tube emerges and into it some of the nuclei move (FIG. 33). Later a second germ tube may appear (FIG. 34). It often fuses with a hypha derived from another spore (FIG. 35). The original spores may contain several nuclei at this and successively later stages. As the hyphae develop the nuclei become dispersed at long intervals and only infrequent septa divide them into multinucleate cells. Conidiophores are produced more or less at right angles as direct outgrowths from a cell of the

mycelium (FIGS. 36, 37), or from the combined products of germ tube anastomoses (FIG. 38), or directly from a single germ tube not concerned with any fusion (FIG. 39). The last condition was one illustrated by De Bary in his 1870 paper. The conidiophore initial is multinucleate and several nuclei move into the developing stalk of the conidiophore where they multiply freely as it elongates and increases in diameter (FIGS. 40, 41). The typical mature conidiophore consists of a terminal dome-shaped vesicle supported on a long stalk which is sometimes septate. It is multinucleate throughout. The stalk becomes vacuolate as the vesicle matures. At that time most of the nuclei are aggregated in the vesicle end. Phialides bud out over the upper surface. As a phialide nears maturity one nucleus moves into it from the vesicle without any alteration in form as the connective between vesicle and phialide is of generous size. The single nucleus of the phialide divides once and one of the two nuclei subsequently passes into the first formed conidium, again without attenuation because of the comparatively large connective between phialide and conidium (FIGS. 42–47). The conidium is separated from the phialide by the deposition of a septum which soon increases into a wide separation band. At the same time a heavy wall is deposited on the outer surfaces. This process gives eventually a series of thick, rough-walled, uninucleate spores (FIG. 48). Several of the nuclei remain in the vesicle and stalk even when many of the spores have been formed, but both structures are by then conspicuously vacuolate. The conidiophores which come directly from spores or unanastomosed hyphae are definitely smaller although their conidia are formed in identical fashion (cf. FIGS. 39 and 41). Such conidiophores resemble the small and short conidiophores found in the *A. glaucus* group on the aerial mycelium. Fundamentally none of these small forms differs from the large type.

The nuclear condition of the conidia in *A. echinulatus* differs greatly from the three species already described. From a comparison of whole mounts (agar-film method) and sections, it is apparent that more than one nucleus moves into the conidium from the phialide on which it is formed. Since the microdimensions of this species are comparatively very large the process of spore formation shows particularly well. The phialides themselves are

multinucleate as nuclei from the vesicle move in abundantly through the ample opening between the two parts, and continue to do so as successive conidia are cut off (FIGS. 49, 50). The first conidium develops as a budding apical protuberance, surrounded by a sheath which is continuous with that over the surface of the vesicle. As the conidium rounds up and its connective with the phialide becomes more pronounced, the sheath becomes noticeably heavier in the connective region and also on the distal surface of the conidium itself. Several nuclei move unchanged through the wide opening (FIGS. 51–53). As many as four nuclei have been seen moving into a spore, and possibly more may enter. Although a cursory glance may suggest that many more than that are moving into the conidium, closer observation shows that several stay in the connective region, the distal portion of which will enlarge to form the next conidium (FIG. 51). Often the nuclei are already in a division stage as they move through the connective region or as they enter the spore, and this adds to the impression of larger numbers of nuclei moving into the spore (FIG. 52) than actually do. Moreover, nuclear divisions in the phialide are infrequently seen. Nuclei continue to move into the phialide from the vesicle as successive conidia of a chain develop. When several conidia have formed in a series it is easy to trace the entire sequence of wall formation. The sheath becomes heavier around the spore but leaves a thinner area between spores so that, upon subsequent separation prior to complete maturity, joined conidia show the sheath becoming echinulate on the free outer surfaces, but still present between them; or if the conidia separate early, the sheath is visible as a little flange (FIGS. 54–56). This is the "disjunctor" region commonly referred to in descriptions of *Aspergillus* spores.

Before a conidium germinates several mitotic divisions have taken place, making it multinucleate unquestionably (FIG. 57). A germinating conidium sends forth a germ tube into which several nuclei move and multiply (FIGS. 58, 59). The number and size of these nuclei are spectacular features of this species. Septa may be laid down in the germ tube near the original spore body, but cross-walls are infrequent typically. A second germ tube from a conidium is not uncommon (FIG. 60). Later (48 hours) some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FIGS. 37–58.

anastomosis among hyphae can be seen. Conidiophores appear at right angles to the assimilative cells, multinucleate from their inception, and enlarge into terminal vesicles which produce a mass of big phialides over their upper surfaces (FIGS. 61–63). The stalks may become one or more septate, a wall often appearing at the base of the vesicle itself. The vesicles have heavy walls with distinct openings into the phialides. The latter show clearly in tangential sections of conidiophores which reveal the openings are from 1–2.5 μ in diameter (FIG. 64). Smaller conidiophores on the aerial mycelium are not unusual. Structurally and cytologically they are identical with the larger ones.

DISCUSSION

This investigation is in agreement with Wakyama's (l.c.) report of uninucleate phialides and conidia in *A. fumigatus* and *A. clavatus,* nor does it disagree with either Dangeard's (l.c.) publication on the former species, or Fraser and Chamber's work (l.c.) on *A. herbariorum* (one of the *A. glaucus* forms). But the results are distinctly at variance with those given by Dale (l.c.) for *A. repens* and by Wakyama for *A. glaucus.* The difficulties attending any investigation in the *A. glaucus* group of *Aspergillus* are complicated by taxonomic confusion. The genus has venerable historic recognition, beginning with Micheli in 1729. He described the readily identifiable "rough-heads" by the name *Aspergillus.* Shortly thereafter *A. glaucus* was described as a species by Link (1809). Thom and Church (1926) used *A. glaucus* to designate a wide-spread group of species with well marked common characteristics that indicate close relationship. Taxonomists concur that specific differences in the *A. glaucus* group are valid only when based upon ascospore characters. Unfortunately there is now no means of determining the type of *A. glaucus* Link since no ascospore descriptions are extant.

Since no definite organism can be assigned specifically to *A. glaucus,* it is difficult to tell with what members of the *A. glaucus* group Fraser and Chambers (l.c.) and Wakyama (l.c.) were actually working. From the ascospore dimensions given by the former workers, it would seem that the species they had was a

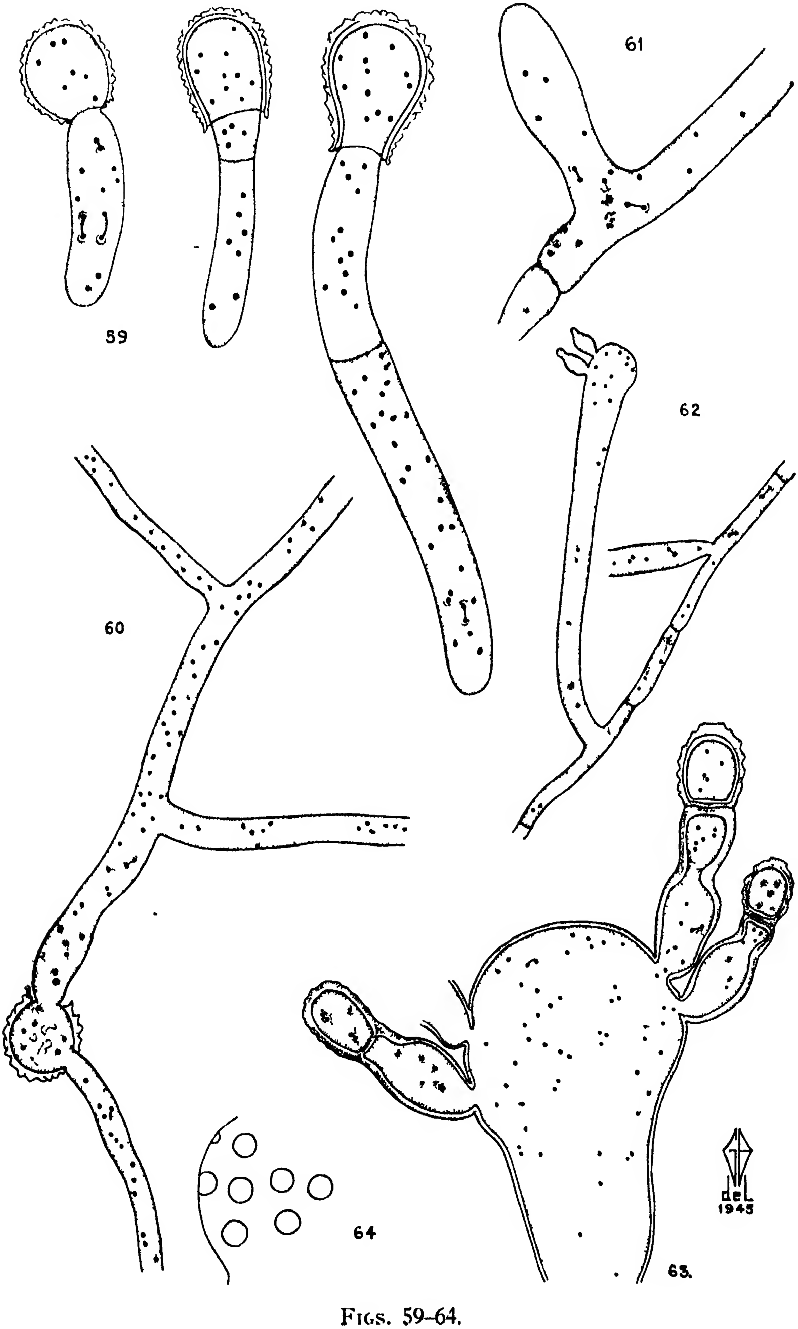
member of the large-spored group, the section in which *A. echinulatus* is classified. Dale's report on *A. repens* emphasizes the similarity of her species and that used by Fraser and Chambers, except for the consistently smaller dimensions of *A. repens*. The identity of *A. repens* does not seem to be in question, so publications relating to that species can be compared directly with this report. But records for *A. echinulatus* can be compared with those on *A. herbariorum* and *A. glaucus* only with the reservation that these forms may not be identical but merely similar.

Dangeard's segregation of *Eurotium* from *Aspergillus* on the basis of nuclear numbers in the conidia is one that has never been widely followed. His cytological figures are not too convincing so it is not surprising that the suggestion had little attention. According to Dangeard the conidia of *E. herbariorum* each contains two to three nuclei. Phialides also were described with four to five nuclei per cell. Fraser and Chambers described the passage of several nuclei to each sterigma (phialide) and several thence to each conidium (*A. glaucus*). At maturity each conidium was said to contain about four nuclei. As seen in *A. echinulatus* each conidium has two or more nuclei entering it but these divide so freely that the mature spore prior to germination may have as many as eight or more nuclei. However, genetically the total number is not so significant as the fact that more than one nucleus is present from the beginning.

According to Dale, *A. repens* has a nuclear history similar to that of *A. glaucus* (*A. echinulatus* of this paper), but her observations could not be confirmed with the *A. repens* examined. There is no doubt that the conidia in the form studied are formed as uninucleate cells but nuclear divisions within the spores make them multinucleate before germination. Not only are the conidia uninucleate at first, but each phialide is also uninucleate and by mitotic divisions provides a nucleus for each successive conidium formed. Dale did not illustrate all stages of conidium production and it is possible that she mistook pre-germination conidia for the formation stage. The cells in this species are small and appearances could easily be misleading. The conidia could be called multinucleate at maturity (before germination) but genetically this is of no importance since all the nuclei are derivatives of one origi-

nal nucleus and therefore are presumably homokaryotic in any one chain of conidia. However, differences could exist between chains as the nuclei entering the conidiophore initial might not be identical. Wakyama (l.c.) reported similar findings for thirteen different species of *Aspergilli* including *A. clavatus, A. fumigatus,* and *A. glaucus.* Again the identity of *A. glaucus* would be open to question. Since both *A. echinulatus* and *A. repens* represent species of the *glaucus* group with demonstrable differences in their nuclear behavior, Wakyama may have been working with a species of the *A. repens* pattern. Whelden (**1940**) likewise found *A. niger* typically had uninucleate phialides and conidia.

It appears that phialides and conidia when first formed in three species of *Aspergilli,* are consistently uninucleate, and that the multinucleate condition in the spores is secondarily derived prior to germination. Consequently if the conidia in these species are homokaryotic in nature it raises the question of the chances of heterokaryosis in such forms. In *Aspergillus fumigatus* by mass spore transfer the mycelial strands as they develop anastomose freely. Eventually multinucleate conidiophores arise from multinucleate segments of the mycelium. Thus if any nuclear variation already exists or is introduced (by mutation) the anastomoses would allow for the redistribution of whatever heterokaryotic types existed. Similarly in *A. clavatus* redistribution can come through anastomoses and the fusions attending the development of the foot-cells. For both of these species the use of monoconidial transfers should perpetuate strictly homokaryotic lines, provided no mutations occur. For *Aspergillus repens,* the third species with uninucleate conidia, single conidial transfers again should reproduce homokaryotic lines, but here the case is complicated because this species represents a homothallic perithecial line, genetically bisexual. The homothallic condition can be shown by single conidium transfers isolated at about the 24 hour stage and transferred to separate petri dishes where they will produce fertile ascocarps and ascospores within two weeks. This is well known for other homothallic perithecial fungi, *e.g., A. Fischeri,* a species similar to *A. fumigatus* (Greene, **1933**); and also many species of *Penicillium* (Emmons and Dodge, **1931**; Dodge, **1933**; Emmons, **1935**). As the usual practice of culture transfer involves the re-



FIGS. 59–64.

moval of many conidia and probably ascospores, the chances of separating out variants are slight by that method. Theoretically karyogamy and meiotic segregation should allow for differences among the nuclei. Presumably then single nucleate conidia should show heterokaryotic differences, for factors not sex-linked.

Finally the fourth species under consideration, *A. echinulatus,* introduces another variable since its conidia are multinucleate from the beginning. It is also a homothallic perithecial form. Single conidium transfers produce ascospores within two weeks, but the growth on the plates is obviously less vigorous than on plates prepared by mass spore transfer. Since the conidia carry several nuclei, theoretically they could be heterokaryotic or homokaryotic depending on the random distribution of the nuclei entering the spores. Therefore one might expect to find differences among cultures derived by single transfer more readily than in the previous instance. Thom and Raper (l.c.) though, have noted that this species is culturally stable as one strain was consistently subculture for 18 years. Probably the transfers involved over the period were by mass spore transfer, which might be the reason for its stability.

Genetically the history of the *Aspergilli* .is still an unknown quantity. Greene's work on *A. Fischeri* (1933), which is homothallic and bisexual, led him to conclude that the differences he noted in cultures derived by single ascospore or single conidial lines, were due to variations and not mutations. His original variants were obtained from single ascospore lines and this might indicate simply that he had segregation of somatic characters not sex-linked. Unfortunately Greene did not do any cytological work, nor was he consistent in his use of conidia or ascospores as the sources of his lines, and neither did he attempt to recombine strains that showed departure from the original types. Ames (1934) has pointed out for *Pleurage anserina* the bisexual nature of the mycelium originating from uninucleate ascospores. Here fertility is controlled by compatibility factors segregating separately. A similar condition might exist in the homothallic *Aspergilli* but there is no experimental evidence on this phase of the problem yet. Until either a thorough cytological investigation is made for one of these homothallic forms, or experimental work on its genetic

behavior is undertaken, it is futile to speculate on the inheritance mechanisms in these fungi. *Aspergillus echinulatus* promises to be a good form for such investigations as the nuclei are of good size and factorial differences may exist in the nuclei entering the conidia. In addition other large spored members of the genus might profitably be investigated to demonstrate the frequency of the *A. echinulatus* type of conidium formation.

SUMMARY

1. In three species of *Aspergillus* (*clavatus, fumigatus,* and *repens*) the conidia are formed as uninucleate cells on uninucleate phialides.

2. The conidium of *A. fumigatus* becomes binucleate by mitotic division preceding germination. This is accompanied by a decided increase in conidium volume. The conidia of the other two species become multinucleate by several mitotic divisions before germination; likewise the spores at germination show great volumetric increase. There is no genetic significance attached to these divisions. In these species the transfer of a single conidium presumably perpetuates a homokaryotic line, but mass spore transfers would allow for the operation of heterokaryosis through anastomoses, dependent upon differences existing in the haploid nuclei. Since *A. repens* is homothallic and perithecial, it might be expected that karyogamy and meiotic segregation would contribute to differences among nuclei, thereby increasing the heterokaryosis.

3. The conidia of *A. echinulatus* are multinucleate when formed, but the original nuclei entering the conidia divide freely so that before germination the cell may have more than eight nuclei. The phialides are also multinucleate. Nuclei continue to pass from vesicle to phialide as conidia are formed. Transfer of a single conidium may mean the carrying of different characters although there is an equal chance that all nuclei which enter the spore are alike.

4. *A. echinulatus* is homothallic and perithecial; consequently the effects of karyogamy and meiotic segregation must be taken into consideration in relation to the nature of the haploid nuclei.

5. In all the species the hyphae become multinucleate when septa

form. Such segments may develop into conidiophore initials either directly or indirectly (foot-cells in *A. clavatus*). There is no way to determine cytologically whether the several nuclei of the conidiophore initial cells are homo- or heterokaryotic. Depending upon this condition, conidia of different chains on the same vesicle may carry like or unlike nuclei.

6. *A. repens* and *A. echinulatus* represent homothallic fungi, as single conidium isolates produce ascospores within two weeks.

7. The nuclear condition of the conidia of these last two species represents a sharp difference in the cytology of two members of the *A. glaucus* group. If they are both good representatives of that group, the suggestion that the group as a whole differs cytologically from other *Aspergilli* is untenable.

The author wishes to express her appreciation to the Department of Biological Sciences at Stanford University for the privileges of its laboratories which greatly facilitated the completion of this investigation.

VASSAR COLLEGE

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EXPLANATION OF FIGURES

All figures drawn with the aid of an Abbé camera lucida. Unless otherwise indicated the magnification is approximately 1850 ×.

Aspergillus fumigatus:

1. Spores, ungerminated and germinating.

2. Spores at 12 hours germination.

3. Spore with two germ tubes and dividing nuclei; 12 hours.

4. Anastomosis between second germ tube of one spore and hypha from another; 25 hours.

5. Stages in development of conidiophore initials; 40 hours.

6. Older conidiophore with portion of nearby assimilative hypha to show difference in diameters; 40 hours.

7. Maturing conidiophore.

8. Expanding vesicle of conidiophore and first appearance of phialides.

9, 10. Stages in phialide development.

11. Mature vesicle with nearly mature phialides on the upper surface, just prior to nuclear migration.

12, 13, 14, 15, 16. A series of phialides showing the entrance of nuclei in the phialide, division, and passage of one nucleus to the conidium.

Aspergillus clavatus:

17. Spores before and after germination; 12 hours.

18. Germination stages at 12 hours.

19. Anastomosis between outgrowths of two conidia with detail of one conidium, × 390 and 900 respectively; 21 hours.

20. Hyphal tip with actively dividing nuclei, × 900; 41 hours.

21. Initial of foot-cell, × 900; 41 hours.

22. Anastomosis of foot-cells, × 900; 41 hours.

23. Young conidiophore, × 900; 41 hours.

24. Older conidiophore with foot-cell, × 900.

25. Expanding vesicle of conidiophore; 59 hours.

26. Apical portion of mature conidiophore, the zone of phialides indicated in outline.

27. Stages in phialide maturation.

28, 29. Division of nucleus in phialide and passage of one nucleus to young conidium.

30. Small conidiophore from aerial hypha.

Aspergillus repens:

31. Spores before and at germination; direct from surface of colony.
32. Germination stages; 23 hours.
33. Later stage in germination; 23 hours.
34. Development of second germ tube; 23 hours.
35. Diagram of anastomosed hyphae from two conidia with young conidiophores, × 435; detail of one cell from hyphal strand at the point indicated, × 900; 31 hours.
36. Stages in development of conidiophore initials; 31 hours.
37. Young conidiophore, the initial completely walled off; 31 hours.
38. Anastomosis between outgrowths of two conidia and developing conidiophore; 23 hours.
39. Small conidiophore from a conidium; 31 hours.

40, 41. Development of vesicle and phialides; 31 hours.

42, 43, 44, 45, 46, 47, 48. A series of phialides showing development and production of conidia; 48 hours.

Aspergillus echinulatus:

49. Phialide with developing conidium.
50. Nuclei moving into conidium; the nuclei in the connective region may be for the next conidium of the series.
51. Nuclei moving into phialide and others moving into conidium.

52, 53. Conidium formation, some nuclei dividing in the young conidia.

54, 55. Maturing conidia in series.

56. Two conidia separated from chain showing disjunctor between them.
57. Mature conidia.
58. Germination of conidium; 22 hours.
59. Germination stages; 22 hours.
60. Hyphal outgrowths from a conidium; 31 hours.
61. Conidiophore at 72 hours.
62. Young conidiophore; 72 hours, × 375.
63. Vesicle with mature phialides and conidia.
64. Phialide openings as seen on surface of vesicle.

STUDIES IN THE GASTEROMYCETES XI. THE GENERA TRICHASTER AND TERROSTELLA

W. H. Long

(WITH 4 FIGURES)

This paper discusses the taxonomic status of three old genera, *Trichaster* Czern., *Geasteropsis* Hollós, and *Geasteroides* Long, reduces *Geasteropsis* to synonymy, renames *Geasteroides*, and redescribes the three species found under these genera.

The *Geasterae* form a well defined group consisting of four genera separated as shown in the following key:

KEY TO GENERA

1. Endoperidium without a sterile base ....(2)
1. Endoperidium with a prominent sterile base ....(1) *Terrostella*
2. Endoperidium persistent, normally with one mouth ....(2) *Geaster*
2. Endoperidium persistent, normally with several mouths ..(3) *Myriostoma*
2. Endoperidium caducous, with a persistent, subligneous columella (4) *Trichaster*

The genera *Geaster* and *Myriostoma* do not need any discussion, but *Trichaster* and *Terrostella* are little known to mycologists. *Trichaster* was discovered and described by Czerniaiev (**1845**) on the Steppes of Russia. Lloyd (**1904**) gives a description and history of this genus, and with his photograph of the type makes it easy to identify. According to Lloyd Czerniaiev sent abundant specimens from the type locality to Berkeley and to Fries.

Trichaster Czern. Bull. Soc. Nat. Moscou **18**^{2}: 149. 1845.

Geasteropsis Hollós, Novenyt. Kozlem. **2**: 72–75. 1903.

Peridium double; *exoperidium* splitting into stellate, reflexed, coriaceous, persistent segments; *endoperidium* fragile, caducous; *columella* persistent, subligneous, compact.

TYPE SPECIES: *Trichaster melanocephalus* Czern.
DISTRIBUTION: Europe; Africa.

TRICHASTER MELANOCEPHALUS Czern. Bull. Soc. Nat. Moscou 18^2: 149. 1845.

Sporophore epigeous, becoming expanded at maturity, 5–8 cm. tall by 3–8 cm. wide; *exoperidium* hard, rigid, coriaceous, splitting beyond the middle into 5–8 unequal rays which bend strongly backward and downward (not fornicate), unsplit area around columella

FIG. 1. *Trichaster melanocephallus* from Moravia.

about 4 cm. in diameter; *rays* sub-hygroscopic, unequal, acute, some of tips slightly revolute; *fleshy layer* 1–2 mm. thick, mummy brown (Ridgway), adnate, continuous; *exterior* naked, smooth, dark brown (russet), no signs of dirt or debris; *base* broad, concave with fragments of a cord-like rhizomorph in center. *Endoperidium* sessile, apparently globose before dehiscence, a few fragments left at base of gleba. *Gleba* subglobose, subsessile with a round thick, sub-ligneous stipe 1.5 cm. broad and expanding above into the regular gleba which is 2–3 cm. high by 2–3 cm. wide, consisting of spores, capillitium and columella; *columella* prominent, persistent, hard, sub-ligneous especially at the base, covered with a matted mass of capillitium and spores; *capillitium* thicker than

spores, 4.5–7 μ thick, walls thin, unbranched, contents tinted; *spores* 4.2–5.2 μ in diameter, globose; *episporc* chestnut brown, verrucose.

TYPE LOCALITY: Ukraine.

HABITAT: Solitary or in small groups on top of ground in deep forests.

DISTRIBUTION: Russia, Ukraine, *B. M. Czerniaiev*, many specimens at Kew, England & at Upsala, Sweden from type locality.

Moravia, Poullauerberge, May 1921, *Dr. J. Hruby*, under the name *Geaster fornicatus*, in F. Petrak, Flora Bohemiae et Moraviae Exsiccata no. 1498 (FIG. 1).

ILLUSTRATIONS: Lloyd, Myc. Writ. **1**: *pl. 17, f. 3.* Ed. Fischer in Engler and Prantl, Nat. Pfl. **7A**: *f. 53, A & B.*

The above description and photograph were made from the Moravian plant, listed above, with some additional data from the original description and from Lloyd's photograph of the type.

I can not find any generic differences between the genera *Trichaster* Czern. and *Geasteropsis* Hollós, both having caducous endoperidia and permanent sub-ligneous columellae. These are the only two characters that differentiate these genera from *Geaster*, and therefore *Geasteropsis* is made a synonym of *Trichaster*; however from the description and figures given by Hollós (l.c.) his *Geasteropsis Conrathi* seems to be different from *Trichaster melanocephalus*.

Trichaster Conrathi (Hollós) comb. nov. (FIG. 2)

Geasteropsis Conrathi Hollós, Novenyt. Kozlem. 2: 72–75. 1903.

Sporophore epigeous, expanded at maturity to about 10 cm. in diameter; *exoperidium* revolute, thick, coriaceous, sub-hygrometric, splitting to about the middle into 10 unequal segments, concave below; *rays* irregular, curved; *exterior* ocher colored, brown and white variegated, longitudinally striate; *fleshy layer* adnate, brown, transversely fissured into corrugations. *Endoperidium* sessile, globose, whitish, soft, flexible, only fragments present which are adhering to the fleshy layer. *Gleba* stipitate, with an angular, stout, sub-ligneous stipe, 12 mm. wide at top, 20 mm. wide at base by 10 mm. tall, expanding above into the regular subglobose,

dark brown, gleba, 3 cm. in diameter, consisting of spores, capillitium and the sub-ligneous columella (FIG. 2). *Columella* firm, subglobose, persistent; *capillitium* subhyaline to dilute brown, rarely branched, non-septate, 4 μ in diameter, walls thick, lumen small; *spores* globose, 1-guttulate, some short pedicellate, 6–8 μ in diameter; *episporc* densely verrucose.

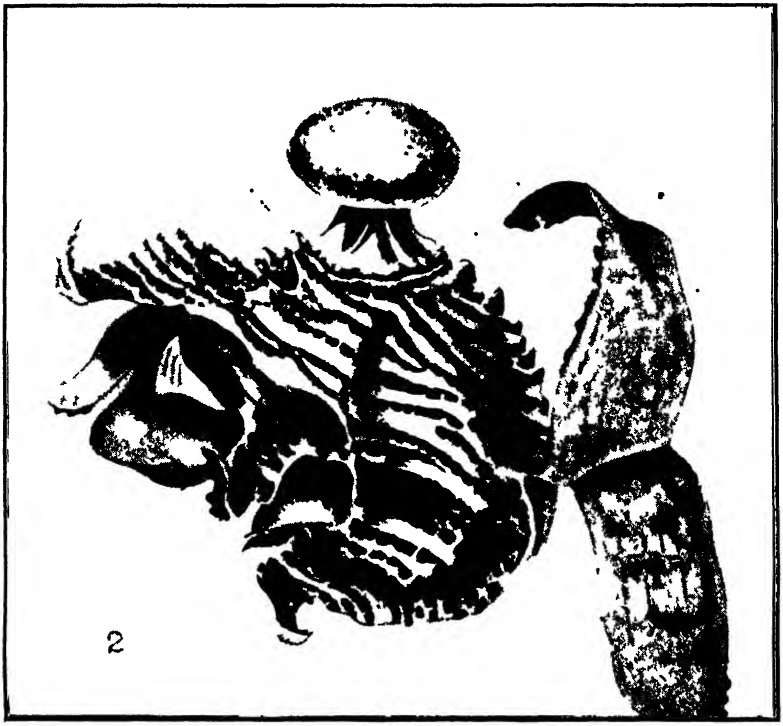

FIG. 2 *Trichaster Conrathi*, dotted circle former position of endoperidium (from Hollos) × 1

HABITAT. In granitic soil on grassy slope, associated with *Welwitschia mirabilis* of the Gnetaceae.

DISTRIBUTION: Union of South Africa, Transvaal, 7½ miles from Johannesburg, elevation 4738 feet, *P. Conrath, 1 specimen,* type of *Geasteropsis Conrathi* Hollós.

ILLUSTRATIONS: Hollós, Novenyt. Kozlem. 2: *pl. 14, f. 1,* and *pl. 15, f. 2–3,* as *Geasteropsis Conrathi.*

The above description and figure were made from the original type description and figures by Hollós.

Ed. Fischer (1933) lists as a new species *Geasteropsis Stahelii*, but no adequate description or figure is given whereby this species can be identified and the name therefore becomes a *nomen nudum*.

Terrostella Long, nom. nov.

Geasteroides Long, Mycologia **9**: 271. 1917.

Peridium double; *exoperidium* splitting into stellate, reflexed, persistent segments; *endoperidium* fragile, upper portion more or less deciduous, lower part persistent, consisting of a prominent sterile base; *mouth* single; *columella* and *capillitium* present.

Terrostella texensis Long, comb. nov. (FIG. 3)

Geasteroides texensis Long, Mycologia **9**: 271. 1917.

Geasteropsis texensis (Long) Ed. Fischer in Engler & Prantl, Pfl. II, **7A**: 75. 1933.

Sporophore hypogeous, buttons not found but apparently acute, judging by the acuminate tips of the expanded exoperidium, becoming superficial and expanded at maturity, then 4–10 cm. in diameter, usual size 6 cm. *Exoperidium* revolute, thick, rigid, coriaceous, sub-hygroscopic, splitting to about the middle into 7–10 segments, concave below, convex above; *rays* unequal, recurved, with strongly involute, acuminate tips, 2–4 cm. long; *exterior* with an outer layer of arachnoid mycelium and dirt that peels off as the plants age, the exposed surface tilleul buff to dingy white, often with faint longitudinal striae; *fleshy layer* adnate, dark brown (carob brown), fissured and cracked when dry, gradually wearing away. *Endoperidium* short stipitate, subglobose, drab gray to light drab, 15–25 mm. broad by 18–20 mm. tall, very fragile, apparently with a poorly defined mouth, upper portion slowly dehiscing down to the sterile base, leaving it crowned with the subglobose columella and spores. *Sterile base* corky, compact, wood brown to fawn color, circular to oblong, circular ones 10–15 mm. across by 8–10 mm. tall, oblong ones 10 × 20 mm. to 25 × 27 mm. across by 10 mm. tall. *Stipe* terete to strongly flattened, stout, subligneous, 2–3 mm. thick by 3–15 mm. wide by 2 mm. high (tall). *Gleba* chestnut brown, in very old plants entirely disappearing and leaving only the sterile base seated on the stipe (FIG. 3); *columella* soft, weak, early deciduous; *capillitium* wine colored to light brown under the microscope, threads very long, distantly branched, 7–10 μ thick, tapering to a slender

FIG. 3. *Terrostella texensis*, sporophores × 1. 4, *Terrostella texensis*, spores and capillitium, × 1000.

point, septate in thicker parts, breaking up into segments 800 to 1000 mμ long, walls smooth, often appearing as if filled with minute pits, lumen very small or none (FIG. 4); *spores* globose, 1-guttulate, 3–5 μ in diameter; *epispore* brown, 1 μ thick, faintly verrucose.

HABITAT: Solitary or in small groups, in rich loose, sandy loam around bases of old rotting post oak stumps (*Quercus stellata*) in open post oak woods.

DISTRIBUTION: Texas, Denton County, west of the Texas State Teachers College, Denton, elevation 620 feet, *W. H. Long*, September 28, 1906, *1671* (*4 plants*), October 8, 1907, *2011 Type* (*14 plants*), October 14, 1907, *2034* (*6 plants*); Pecan Creek near Denton, October 14, 1907, *2035* (*3 plants*).

These specimens were collected in three different localities in the vicinity of Denton; Nos. *2011* and *2034* were found 2 miles from the location of the first collection No. *1671*.

The distinguishing features of this species are its prominent, corky sterile base and its fragile deciduous endoperidium. Specimens are deposited as follows: 6 plants from type material in the Lloyd Myc. Col. No. *8787* as *Trichaster texensis,* a herbarium name; 4 plants from type material are in the Herbarium of the University of California at Berkeley, No. *53941,* under the name *Geasteroides texensis;* the remainder of the collections are in the Long Herbarium at Albuquerque, N. Mex.

The generic name *Geasteroides* is untenable since it is already preoccupied by Battarra's genus (**1755**) of same name, and especially since Ed. Fischer (l.c.) has revived this name as a synonym for *Geaster.* I am therefore changing the generic name of this fungus to *Terrostella* nom. nov.

ACKNOWLEDGMENTS

I am indebted to Mr. John A. Stevenson for the loan of material and many helpful suggestions and to Dr. David H. Linder for valuable suggestions on nomenclature.

ALBUQUERQUE, NEW MEXICO

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ADDITIONS TO THE UREDINALES REPORTED FOR PERU [1]

George B. Cummins

(with 5 figures)

The Uredinales reported in this paper were collected, for the most part, by Macbride and Featherstone and were made available for study by Dr. Francis Drouet, the Chicago Natural History Museum. All specimens are deposited in the Chicago Natural History Museum, with duplicates in the Arthur Herbarium of the Purdue University Agricultural Experiment Station. Species of rusts or of hosts marked with an asterisk are those not recorded by Garcia Rada and Stevenson (La Flora Fungosa Peruana. 112 pp. 1942. Lima, Peru).

***Aecidium mitoense** sp. nov.

Pycniis non visis. Aeciis hypophyllis, subepidermalibus, in greges minutos aggregatis vel plerumque sparsis, flavidis, 275–350 μ diam., cupulatis, margine recurvato; cellulis peridii flavidis oblongis, 17–24 × 49–68 μ, pariete exteriore minute verrucoso 4.5 μ cr., interiore 2 μ cr.; aeciosporae globoideae vel ellipsoideae, 18–23 × 22–31 (–35) μ; membrana 2.5–3.5 μ cr., minuteque verruculosa, flavida vel pallide aurea.

On *Sessea stipulata* R. & P., Mito, Peru, July 8–22, 1922, *Macbride & Featherstone 1487* (type). Alt. 9000 ft.

The aecia of this species characteristically occur rather widely scattered, frequently singly and seldom with more than a few sori in a group. Yellowish spots develop on the leaves where the aecia are grouped but they are usually small and inconspicuous. The long yellowish peridial cells are somewhat reminiscent of *Roestelia* but with finer markings than most species of that form-genus.

*Aecidium Fuchsiae Jacks. & Holw. *Fuchsia denticulata* R. & P., Muña, June 5–7, 1923, *Macbride 4285.*

[1] Journal Paper Number 217, of the Purdue University Agricultural Experiment Station. Contribution from the Department of Botany and Plant Pathology.

*AECIDIUM sp. *Baccharis alpina* H.B.K., Rio Blanco, Mar. 20–25, 1923, *Macbride 3024*. Alt. 15,000 ft.

This collection probably represents an undescribed species but it is too fragmentary to name. Aecia occur on the undersides of the leaves, evenly and closely scattered over the entire surface of all terminal leaves of a branch. This indicates that the infection is at least locally systemic whether perennial or not. The aecia are cupulate with an erose or slightly recurved margin, yellowish, and about 0.2 mm. in diameter. Aeciospores are globoid or occasionally ellipsoid, 17–19 × 19–23 (–25) μ with a yellowish, finely verrucose wall 1 μ in thickness.

*CEROTELIUM ? sp. *Halenia umbellata* (R. & P.) Gilg, Mito, July 8–22, 1922, *Macbride & Featherstone 1658*. Alt. 9000 ft.

This interesting but fragmentary specimen represents an undescribed species of questionable relationship. The rust is apparently microcyclic and devoid of pycnia. No species of similar morphology has been recorded on the Gentianaceae, nor have microcyclic species of unquestioned affinity been described in the genus *Cerotelium*.

Telia hypophyllous, subepidermal, densely gregarious in groups 3 mm. in diameter or up to 5 mm. in length along the midrib, individual sori small, round 0.2–0.4 mm. in diameter, reddish and waxy in appearance becoming yellowish and somewhat farinaceous with maturity, 4–8 spores in thickness, without peridium or paraphyses; teliospores catenulate in origin but not firmly united either laterally or apically and therefore not in discrete strata or chains, oblong or ellipsoid, 10–15 × 22–32 μ (or smaller in immature condition); wall uniformly 1 μ or less in thickness, smooth, hyaline or essentially so.

CHRYSOCELIS LUPINI Lagerh. & Diet. *Lupinus *bogotensis* Benth., Huariaca, Apr. 3, 1923, *Macbride 3118; L. *humifusus* Benth., Mito, Aug. 1–5, 1922. *Macbride & Featherstone 1817; L. *mutabilis* Sims, Uspachaca, June 23, 1922, *Macbride & Featherstone 1301*.

*CHRYSOPSORA GYNOXIDIS Lagerh. (FIG. 1.) *Gynoxys* sp., Mito, Aug. 1–5, 1922, *Macbride & Featherstone 1842*.

The host was determined as *Sessea* but, because of the characteristic morphology of the rust, I am confident that the plant must be

a species of *Gynoxys*. It compares closely with specimens of *Gynoxys* in the Arthur Herbarium.

COLEOSPORIUM IPOMOEAE (Schw.) Burr. *Ipomoea *angulata* Lam., La Merced, Aug. 10–24, 1923, *Macbride 5340; I. purpurea* Lam., Huanuco, Apr. 5–8, 1923, *Macbride & Featherstone 3211,* Apr. 28, 1923, *Macbride 3532.*

KUEHNEOLA LOESENERIANA (P. Henn.) Jacks. & Holw. *Rubus *floribundus* H.B.K., Mito, July 8–22, 1922, *Macbride & Featherstone 1406; R. *roseus* var. *rosaeflorus* Hook., and var. *santarosensis* (Ktze.) Macbr., Muña, June 5–7, 1923, *Macbride 4287, 4289.*

MAINSIA HOLWAYI Jacks. *Rubus *bogotensis* H.B.K., Panao, May 10, 1923, *Macbride 3604; R. *floribundus* H.B.K., Mito, Aug. 10, 1922, *Macbride & Featherstone 1940; R. floribundus* var. **nimbatus* Mack., Yanahuanca, June 16–22, 1922, *Macbride & Featherstone 1219.*

PUCCINIA ABRUPTA Diet. & Holw. *Viguiera Pflanzii* Perkins, Mito, July 8–22, 1922, *Macbride & Featherstone 1535; V. *pusilla* (Gray) Blake, Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 471.*

*Puccinia abutiloides sp. nov. (FIG. 2)

Pycniis, aeciis, et urediis nullis. Teliis subepidermalibus, hypophyllis, sparsis vel laxe aggregatis, rotundatis, usque ad 2.5 mm. diam., pulverulentis, cinnamomeo-brunneis vel obscurioribus, epidermide rupta plus minusve conspicue; teliosporae ellipsoideae, utrinque rotundatae, medio non vel vix constrictae, 23–29 × 33–45 µ; membrana uniformiter 3.5–4.5 µ crassa, cinnamomea vel pallide castanea, moderate verrucosa vel plus minus reticulato-verrucosa; poro superiore apicali, inferiore infra medium loculum sito; pedicello hyalino, fragili, brevissimo.

On *Abutilon virgatum* Sweet, Huanuco, Peru, Apr. 25, 1923, *Macbride & Featherstone 3494* (type). Alt. 7000 ft.

Telia of this species are paler brown, larger, and less inclined to occur in groups than is true of the telia of *Puccinia Abutili* Berk. & Br. The lower germ pore is close to the pedicel in both species and the size and shape of the spores are similar. However, the markings are conspicuously coarser in *P. abutiloides,* more irregular in shape and frequently are labyrinthiformly united or tend to

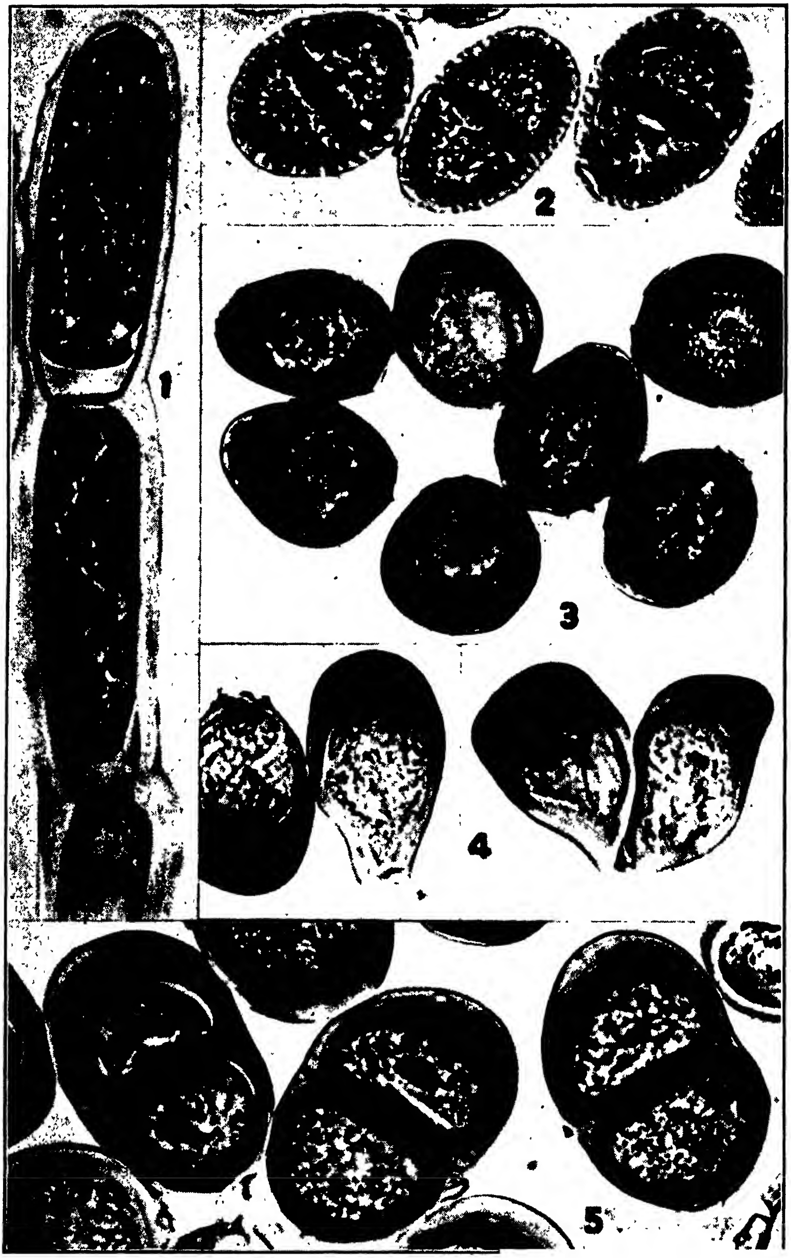


FIG. 1–5

occur in longitudinal lines. No American rust of Malvaceae is similar to *P. abutiloides.*

PUCCINIA ARISTIDAE Tracy. *Aristida adscensionis* L., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 341.*

*PUCCINIA BIMBERGI Mayor. *Heliopsis canescens* H.B.K., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 473a.*

*PUCCINIA BOMAREAE (Lagerh.) P. Henn. *Bomarea ovata* (Cav.) Mirb., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 353; B. tarmensis* Kränzl., Cueva Grande, June 23, 1923, *Macbride 4781.*

PUCCINIA CONOCLINII Seym. *Ageratum *conyzoides* var. *inaequipaleaceum* Hieron., Llata, Aug. 21, 1922, *Macbride & Featherstone 1997; Eupatorium *Kalenbornianum* Rob., Yanahuanca, June 16–22, 1922, *Macbride & Featherstone 1176, 1197,* San Rafael, Apr. 4, 1923, *Macbride 3135.*

*PUCCINIA CONTURBATA Jacks. & Holw.? *Salvia punctata* var. *glabra* Epl., Mito, July 8–22, 1922, *Macbride & Featherstone 1398, 1662.*

Both collections are meager. The rust is generally similar to *P. conturbata* but the germ pore in the lower cell of the teliospore is near the pedicel.

PUCCINIA CRASSICUTIS Syd. *Mutisia viciaefolia* var. *hirsuta* (Meyen) Wedd., Tarma, June 1–6, 1922, *Macbride & Featherstone 1015.*

*PUCCINIA DICHONDRAE Mont. *Dichondra repens* Forst., Chasqui, Apr. 10, 1923, *Macbride 3303.*

*PUCCINIA FESTATA Jacks. & Holw. *Euphorbia* sp., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 86.*

This species has been reported previously only from Ecuador.

PUCCINIA HETEROSPORA Berk. & Curt. *Anoda hastata* Cav., Llata, Aug. 21, 1922, *Macbride & Featherstone 1996.*

*PUCCINIA HIERACII (Schum.) Mart. *Hypochoeris sessiliflora* H.B.K., Rio Blanco, May 8–19, 1922, *Macbride & Featherstone 745.*

FIG. 1. Teleospore of *Chrysopsora Gynoxidis:* only the upper portion of the long, stout pedical is shown; 2, Teliospores of *Puccinia abutiloides* (from type); 3, Teliospores of *Uromyces Suksdorfii;* the spores are finely verrucose; 4, Teliospores of *Uromyces araucanus;* 5, Teliospores of *Puccinia Macbrideana* (from type), × 800.

*PUCCINIA IMPEDITA Mains & Holw. *Salvia occidentalis*, Huanuco, Sept. 23, 1922, *Macbride & Featherstone 2380.*

*PUCCINIA MINUSCULA Arth. *Helianthus Jelskii* Hieron., Yanahuanca, June 16–22, 1922, *Macbride & Featherstone 1199.*

The uredia in this collection have long, hyaline, thin-walled, cylindrical or clavate, peripheral paraphyses measuring 12–35 × 100–200 μ. When telia develop in old uredia they also have paraphyses but their presence could not be demonstrated in telia showing no urediospores. This may account for the fact that paraphyses are not mentioned in the original description or they may have been overlooked, since they can be confused with leaf hairs.

PUCCINIA MOGIPHANIS (Juel) Arth. *Alternanthera* **calcicola* Standl., La Oroya, May 27–June 7, 1922, *Macbride & Featherstone 961; A. *porrigens* (Jacq.) Kuntze, Ambo, June 28, 1922, *Macbride & Featherstone 1348*, Huanuco, Apr. 26, 1923, *Macbride & Featherstone 3497.*

*PUCCINIA PUNCTATA Link. *Relbunium hypocarpium* (L.) Hemsl., Mito, July 8–22, 1922, *Macbride & Featherstone 1373.*

PUCCINIA ROSEANA Arth.? *Fourcroya *andina* Trel. and *F. *occidentalis* Trel., Matucana, Mar. 14–18, 1923, *Macbride 2923.*

A meager collection consisting of aecia.

PUCCINIA RUBIGO-VERA (DC) Wint. **Thalictrum podocarpum* H.B.K., Cuzco, Dec. 1928, *Herrera 1528a.*

*PUCCINIA SARACHAE Mayor. *Saracha biflora* R. & P., Cani, Apr. 16–26, 1923, *Macbride 3444*

***Puccinia Satureiae** sp. nov.

Pycniis subepidermalibus, epiphyllis, globoideis, 150–180 μ diam., paraphysatis. Aeciis subepidermalibus, hypophyllis, in greges usque 1.5 mm. diam. aggregatis, frequenter circinatim dispositis, flavidis, cupulatis, 150–185 μ diam.; cellulis peridii pallide flavidis, 17–26 × 36–45 (–60) μ, pariete exteriore 2 μ cr., interiore moderate verrucoso 4–6 μ cr.; aeciosporae late ellipsoideae vel ellipsoideae, 20–26 × 26–30 (–36) μ; membrana pallide flavida, 1.5 μ cr., moderate verrucosa. Urediis non visis verissimiliter nullis. Teliis hypophyllis, sparsis, pulvinatis, rotundatis, 0.1–0.3 mm. diam., aureo-brunneis; teliosporae oblongo-ellipsoideae vel plus minus cylindraceae, utrinque rotundatae, medio vix constrictae, 17–20 (–23) × 53–65 (–73) μ; membrana flavida, uniformiter 1 μ cr., levi; pedicello plus minusve sporam aequante, hyalino.

On *Satureia Pavoniana* Briq., Mito, Peru, July 8–22, 1922, *Macbride & Featherstone 1443* (type). Alt. 9000 ft.

Differentiated germ pores appear not to be formed. Germination of the teliospores occurs without a rest period. The basidium is formed at the apex of the upper cell and next to the septum in the lower cell.

PUCCINIA SHERARDIANA Körn. *Abutilon *sylvaticum* (Can.) Schum., Huacachi, May 20–June 1, 1923, *Macbride 4157.*

PUCCINIA SPILANTHICOLA Mayor. *Spilanthes ciliata* H.B.K., Huanuco, Apr. 28, 1923, *Macbride & Featherstone 3527.*

***Puccinia Macbrideana** sp. nov. (FIG. 5)

Pycniis et aeciis ignotis. Urediis amphigenis subepidermalibus, obscure cinnamomeo-brunneis, pulverulentis, sparsis, rotundatis vel ellipsoideis, usque 1 mm. longis, epidermide rupta conspicue; urediosporae late ellipsoideae vel ellipsoideae, 22–27 × 28–35 μ; membrana 2.5–3 μ cr., cinnamomeo-brunnea, moderate echinulata; poris germ. 4–6, sparsis. Teliis amphigenis subepidermalibus, sparsis vel laxe aggregatis, frequenter plus minusve confluentibus, castaneo-brunneis, pulvinatis, rotundatis, 0.5–1.5 mm. diam.; teliosporae late ellipsoideae vel ellipsoideae, utrinque rotundatae, medio non vel vix constrictae, 29–40 × 43–58 μ; membrana castaneo- vel pallide castaneo- vel aureo-brunnea, 3–5 μ cr., ad apicem 7–9 μ, levi; poro superiore apicali, inferiore juxta septum sito; pedicello hyalino, usque ad 80 μ longo sed plus minusve fragili et frequenter deciduo.

On *Baccharis Sternbergiana* Steud., Llata, Peru, Aug. 21, 1922, *Macbride & Featherstone 1992* (type). Alt. 7000 ft.

Puccinia Macbrideana has a general resemblance to *P. unicolor* Arth. but has larger telia, somewhat larger teliospores whose walls are darker in color, and uredia which are dark brown and much larger. The urediospores, too, differ strikingly from those of *P. unicolor* because of their cinnamon-brown color, thick walls, and coarser echinulation. Germ pores in the urediospores are covered with slight cuticular umbos and while relatively large are not readily observable.

PUCCINIA sp. *Geum?* sp., Muña, trail to Tambo de Vaca, June 5–7, 1923, *Macbride 4316.*

Uncertainty concerning the identity of the host and the meagerness of material make it impossible to do more than record the characteristics of this rust.

Pycnia epiphyllous, subepidermal, few in a group, depressed globoid or lenticular, 135–165 μ wide, 60–90 μ high, with short and inconspicuous paraphyses. Aecia mainly epiphyllous, subepidermal, without paraphyses, uredinoid, circinately confluent in a ring, 1–1.5 μ in diameter, around the pycnia, yellowish, pulverulent, ruptured epidermis conspicuously elevated; aeciospores mostly ellipsoid, 19–25 × 29–35 (–37) μ; wall hyaline or pale yellowish, 2–3 μ thick, echinulate with stout spines 2–2.5 μ long; pores obscure, perhaps equatorial. Uredia not distinguished with certainty, if present differing from the aecia only in the scattered distribution and hypophyllous position. Telia hypophyllous, scattered, pulvinate, chestnut-brown, round, 0.2–0.4 mm. in diameter; teliospores somewhat variable but mostly ellipsoid or clavate-ellipsoid, rounded at the apex, rounded or narrowed at the base, slightly constricted at the septum, 25–31 (–35) × 42–55 (–59) μ; wall 2 μ thick at sides, light chestnut-brown, thickened to 4–7 μ over the pores by a semihyaline umbo, finely and evenly verrucose; germ pore apical in the upper cell, next the septum in the lower cell; pedicel hyaline or yellowish, thin-walled, about as long as the spore, mainly persistent. The teliospores germinate without a period of rest.

***Uredo Arcytophylli** sp. nov.

Urediis subepidermalibus, hypophyllis, pulverulentis, cinnamomeis, sparsis, ellipsoideis, 0.3–0.8 mm. longis, epidermide rupta conspicue; urediosporae late ellipsoideae, ellipsoideae vel oblongo-ellipsoideae, 19–25 (–29) × 29–33 (–36) μ; membrana 1.5–2 μ cr., cinnamomea vel pallide cinnamomea, minuteque echinulata; poris 6–8, plus minusve obscuris.

On *Arcytophyllum thymifolium* (R. & P.) Standl., Tarma, Peru, June 1–6, 1922, *Macbride & Featherstone 1013* (type). Alt. 7000 ft.

The pores are difficult to observe with accuracy but usually occur more or less in the equatorial region but not in distinct bands. There are apparently three or four one side of the spore and an equal number on the opposite side, the spores somewhat flattened on the pore-bearing sides.

UREDO IRREQUISITA Jacks. & Holw. *Verbesina *Sodiroi* Hieron., Chinche, June 21, 1922, *Macbride & Featherstone 1257.*

*UREDO sp. *Manettia peruviana* Standl., Mito, July 8–22, 1922, *Macbride & Featherstone 1442.*

Uredia in this specimen are amphigenous and cinnamon-brown, the spores obovate with the base rather broad, 24–27 × 27–33 μ, the wall moderately echinulate, 1.5 μ thick, cinnamon-brown, and provided with two basal pores. The collection may possibly be referable to *Goplana andina* Syd. described on *Manettia Lobbii* from Ecuador. Germ pores in *G. andina* are described as obscure.

UREDO sp. *Alternanthera elongata* (Willd.) Schinz., San Rafael, Apr. 4, 1923, *Macbride 3139.*

While similar macroscopically to the uredia of *Puccinia mogiphanis* (Juel) Arth. this rust differs in having closely echinulate spores with three strictly equatorial pores. *Uredo Alternantherae* Jacks. & Holw. has echinulate spores but scattered pores. Spores in the above collection measure 26–30 × 30–35 μ, with a cinnamon-brown wall 2.5 μ thick.

*UROMYCES ARAUCANUS Diet. & Neger. (FIG. 4.) *Senecio* sp., Yauli, May 25, 1922, *Macbride & Featherstone 923.* Alt. 13,500 ft.

No material has been available for comparison and this collection is identified with *U. araucanus* with uncertainty. The sori occur in confluent groups 2–5 mm. in diameter, the individual sori early merging to form a continuous sorus, chestnut-brown, compact, and only loosely covered by the ruptured and somewhat shredded epidermis. Such characteristics do not agree well with the description of *U. araucanus.* The spores appear to be similar, measuring 20–27 × 33–43 μ, with an occasional spore much larger. The wall is chestnut-brown, 2–3 μ at the sides and 6–9 μ at the apex. Pedicels are hyaline rather than brownish as in *U. araucanus.*

UROMYCES BIDENTICOLA (P. Henn.) Arth. *Bidens *leucanthema* (L.) Krause, Huanuco, Sept. 23, 1922, *Macbride & Featherstone 2318a; B. pilosa* var. *dubia* (Cass.) O. E. Schulz, Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 170.*

*UROMYCES COMMELINAE (Speg.) Cooke. *Tradescantia cymbispatha* Clarke, Mito, July 8, 1922, *Macbride & Featherstone 1616.*

*UROMYCES CUCULLATUS Syd. *Baltimora recta* L., La Merced, Aug. 10–24, 1923, *Macbride 5456.*

*UROMYCES ERAGROSTIDIS Tracy. *Eragrostis pilosa* (L.) Beauv., Apr. 12–May 3, 1922, *Macbride & Featherstone 394.*

*UROMYCES HEDYSARI-PANICULATAE (Schw.) Ellis. *Desmodium uncinatum* (Jacq.) DC., Cabello, June 25, 1922, *Macbride & Featherstone 1332.*

UROMYCES LATHYRINUS Speg. **Vicia Matthewsii* Gray, Rio Blanco, Mar. 20–25, 1923, *Macbride 2964.*

UROMYCES PROËMINENS (DC.) Pass. *Euphorbia *geniculata* Ortega, Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 274; E. lasiocarpa* Kl., Rio Huallaga Cañon, June 3, 1923, *Macbride 4231; E. *rhytisperma* Engelm., Matucana, Apr. 12–May 3, 1922, *Macbride & Featherstone 201.*

*UROMYCES SPHAERICUS Jacks. & Holw. *Perymenium ecuadoricum* Blake, Huanuco, Apr. 28, 1923, *Macbride & Featherstone 3525.*

UROMYCES STRIATUS Schroet. *Medicago *lupulina* L., Mito, July 8–22, 1922, *Macbride & Featherstone 1558.*

*UROMYCES SUKSDORFII Diet. & Holw. (FIG. 3.) *Silene chilensis* (Gay) Cham. & Schlecht., Rio Blanco, Mar. 20–25, 1923, *Macbride 2962.*

This specimen, collected at an altitude of 15,000 ft., has more finely verrucose teliospores than most previous collections but is undoubtedly too closely related to segregate as a species. *U. Suksdorfii* has not been reported previously south of the United States.

*UROMYCES TENUISTIPES Diet. & Holw. *Desmodium mollicula* (H.B.K.) DC., Mito, July 8–22, 1922, *Macbride & Featherstone 1371.*

*UROMYCES TRIFOLII-MEGALANTHI (Diet. & Neger) Jacks. & Holw. *Trifolium peruvianum* Vog., Rio Blanco, May 8–19, 1922, *Macbride & Featherstone 750.*

THE ARTHUR HERBARIUM,
PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION,
LAFAYETTE, INDIANA

TWO NEW GENERA OF RUSTS ON BIGNONIACEAE

B. B. Mundkur and M. J. Thirumalachar

(with 8 figures)

A rust on *Stereospermum suaveolens* was placed in the genus *Phakopsora* by Mundkur (1943) who claimed that he had found the aecial stage which, until then, was unknown for the genus. A re-examination of the rust has now revealed that what he claimed to be aecia are merely the immature stages of the telia and that the rust itself does not fit into the genus *Phakopsora*. A new genus has been established to accommodate the rust and named *Mehtamyces*, for Dr. K. C. Mehta, a distinguished Indian Cereal Rust Pathologist.

The rust is a hemiform with pulverulent, subepidermal uredia. Dr. G. B. Cummins of the Arthur Herbarium to whom a specimen was sent wrote to say that the uredia and the urediospores closely resemble and in fact are identical with those of *Uredo Stereospermi* Sydow, recorded on *Stereospermum chelonoides* (L.f.) DC. He also wrote that the rust did not appear to him to be a typical *Phakopsora* and suggested that a new genus may have to be established for its accommodation.

This re-examination has confirmed that view. Bits of the herbarium material were softened for a detailed microtome study and good sections were obtained. They were stained with safranin using light green as counter-stain. The material is very old, still the degenerated nuclei within the teliospores could be made out. There were two of them in the young teliospores and a single fusion nucleus in the mature ones.

The urediospores are pedicellate and are formed in clusters on sporogenous basal cells. This feature has already been pointed out by Cummins (1940) for *Uredo Stereospermi*. The development of urediospores in clusters on sporogenous basal cells, the

presence of bilaminate wall with bicapitate apex strongly suggest the characters of the genus *Prospodium*. That genus is, so far as it is at present known, confined to the Western Hemisphere and Cummins did not, in the absence of the telial stage, transfer *Uredo Stereospermi,* a step which was very wise.

The telia, which distinguish the rust from *Prospodium,* are subepidermal and non-erumpent, the infection patches being circular to irregular in outline, slightly raised and black and up to 3 cm. in diameter. Sections through the telia indicate that they are mostly epiphyllous, very rarely amphigenous. The sori (FIG. 1) are formed between the epidermis and the palisade layers by the concentration of the hyphae. The sorus is not limited in outline as it becomes indefinite by the confluence of the infection patches. The teliospores are formed from the base of the sori in regular chains. The young spores are rectangular, thin-walled, somewhat hyaline, showing two distinct nuclei (FIG. 2), which on account of the age of the specimens present a shrivelled appearance. Mature spores are cuboid to rectangular (FIG. 3), yellowish-brown, smooth and measure 13–33 × 8–15 μ. Immature telia resemble caemoid aecia that have not erupted, which led Mundkur (**1943**) into an error. Mature spores get dispersed by the disintegration of the host tissue.

The occurrence of subepidermal uredia and of urediospores borne in clusters on sporogenous cells, taken along with telia which occur in subepidermal non-erumpent crusts with teliospores in regular chains, indicates that the rust cannot be accommodated in any of the rust genera so far described. In the type of uredia and of urediospores it completely resembles species of *Prospodium* in possessing clustered urediospores whose wall is bilaminate with a bicapitate apex. The telia themselves to a certain extent resemble the telia of *Angiopsora* in having catenulate teliospores but differ in not being lenticular; in fact they are definite. These combinations of characters justify the erection of the genus *Mehtamyces.*

Mehtamyces gen. nov.

Pycnia and aecia unknown. Uredia subepidermal, aparaphysate; urediospores borne in clusters on sporogenous basal cells; walls bilaminate. Telia in subepidermal crusts, non-erumpent,

indefinite; teliospores developed in chains, basipetally; germination unknown.

Type species: *Mehtamyces Stereospermi* (Mundkur) Mundkur & Thirumalachar.

Pycnia atque aecia ignota. Uredia subepidermalia, aparaphysata; uredosporae catervatim ortae ex sporogenis basicis cellulis, parietibus bilaminatis. Telia in crustis subepidermalibus, haud erumpentia, indefinita; teliospora catenatim basim versus productae; germinatio ignota.

Species typica; *Mehtamyces Stereospermi* (Mundkur) Mundkur et Thirumalachar.

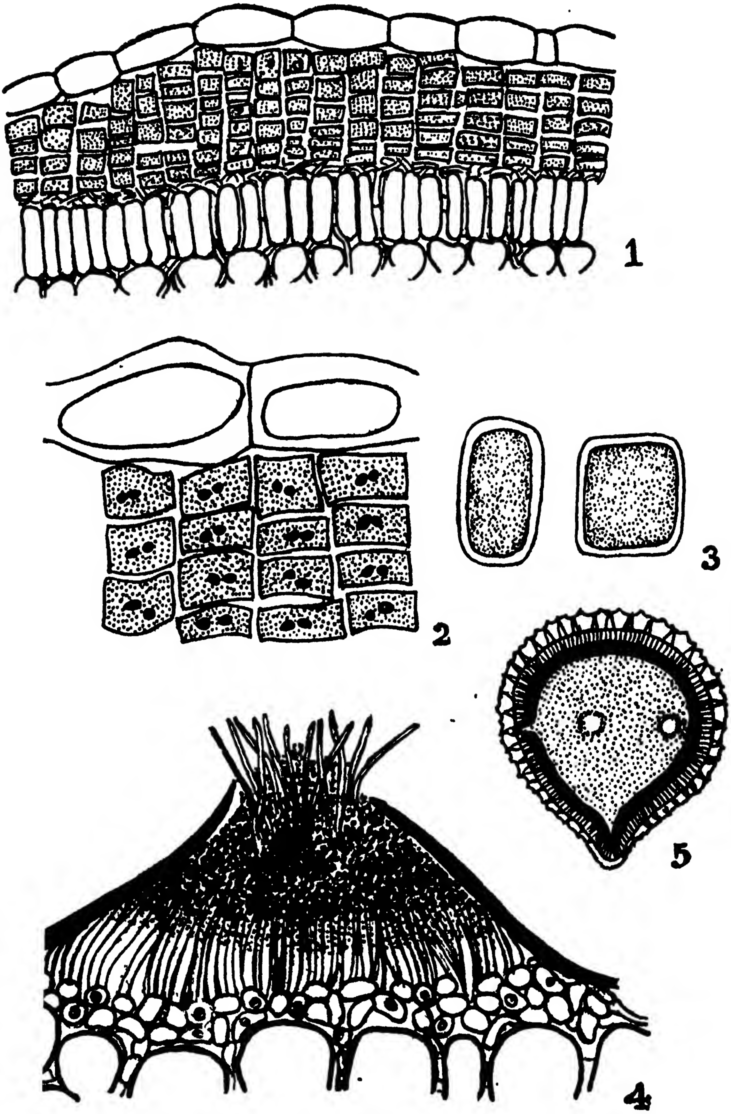
Mehtamyces Stereospermi (Mundkur) comb. nov.

Uredo Stereospermi Sydow, Ann. Myc. **13**: 37. 1915.
Phakopsora Stereospermi Mundkur, Mycologia **35**: 542. 1943.

Uredia amphigenous, mostly hypophyllous, sparse, pale-yellowish brown; urediospores obovate-ellipsoid, with two approximately equatorial germ pores, 24–35 × 19–25 μ; inner wall yellowish, up to 2 μ thick, outer phaline and hygroscopic, up to 7 μ thick, investing the spores in the form of a band between the pores and being bicapitate at apex; sparsely echinulate. Telia circular to irregular in outline, black, slightly raised, indefinite, non-erumpent, aparaphysate; teliospores in chains of 4 to 8 spores, formed between the epidermis and palisade layers, yellowish brown, rectangular to cuboid, 13–33 × 8–15 μ; wall up to 2.5 μ thick.

On living leaves of *Sterospermum suaveolens* Wall. Nagpur (Central Province), 17–9–1922, coll. R. T. Pearl (Type); type deposited in *Herb. Crypt. Ind. Orient.*

In 1943 Rev. Father H. Santapau, S.J., Professor of Botany, St. Xavier's College, Bombay, collected a rust on *Heterophragma Roxburghii* at Khandala, near Poona. The rust occurs in great abundance in the Western Ghats and field observations by Father Santapau have shown that affected trees are severely defoliated. One tree growing in the Government Botanic Garden at Bangalore also showed severe infection and afforded an opportunity for watching the various stages in the life cycle of the rust. For morphological study the material was fixed in formalin acetic alcohol and the microtome sections were stained with Newton's iodine gentian violet.



FIGS. 1–5. *Mehtamyces Stereospermi.*

The rust is an autoecious eu-form occurring throughout the year, mostly in the uredial stage. The leaves are completely covered over their surface by the pustules and the powdery masses of urediospores form clouds of dust when the trees are violently shaken.

The pycnia (FIG. 4) are formed soon after the telial stage is over in the month of December. Leaves bearing the telia drop to the ground and when collected the next morning, after a heavy dew fall, show abundant teliospore germination. The sporidia infect the young, newly formed leaves of the host and the infection spot appears as a crimson yellow speck, gradually becoming swollen and pulvinate. By about the tenth day, numerous pycnia develop in concentric rings on both sides of the infection spot. Pycnia are amphigenous, subcuticular, conoid and slightly compressed. A few ostiolar filaments emerge but they are embedded in nectar containing numerous pycnospores. Nectar is secreted in copious quantities.

The aecia (primary uredia) soon replace the pycnia and are uredinoid (FIG. 6). They are mostly epiphyllous and only occasionally amphigenous, subcuticular, erumpent and pulverulent. Due to the confluence of the infection patches, the sori become indefinite. From the base of the sori binucleate hyphae which are cylindric emerge out, breaking through the cuticle. From their tips are formed the young aeciospores which resemble the urediospores. Mature spores are obovate to ellipsoid with a bilaminate wall. The inner wall is golden brown, up to 5 μ thick; the outer wall is hyaline, hygroscopic, forming a band on one side, thus resembling the unicapitate type of spores of some species of *Prospodium*. Three distinct germ pores situated about the equator can be observed. The aeciospores germinate readily when placed in drops of water in a moist chamber.

The uredia (secondary uredia) follow the aecia in development. They are also amphigenous, and can be differentiated from the aecia by their subepidermal nature (FIG. 7). The uredial initials are formed beneath the epidermis and, as development takes place, stipitate urediospores borne singly on pedicels are formed, which resemble the aeciospores (FIG. 5). Even though little difference exists between the aeciospores and the urediospores, still the aecia

are always associated with the pycnia whereas the uredia are grouped with the telia.

The telia are formed only between the months of September and December. The telia are amphigenous, subepidermal and erumpent. Mature telia occur as waxy rusts, the spores being formed in regular chains which on rupturing appear as short columns (FIG. 8). The mature telium becomes slightly pulverulent at the apex as in *Cerotelium* and the spores also show a tendency to get separated. In a young telium the binucleate cells organize themselves as subepidermal crusts and they very much resemble the telial crusts of *Melampsora.* Very soon more spores are abstricted basipetally and in chains which coalesce laterally to form short columns. Mature spores are hyaline to pale cinnamon yellow, with a prominent fusion nucleus which can be seen in stained preparations.

The type of structure and the manner of development of the teliospores in this rust closely resemble the condition present in the genus *Cerotelium.* According to Mains (**1921**) the genus *Cerotelium* includes those rusts alone which have subepidermal uredia lined with a peridium or hyphoid paraphyses and sessile urediospores and telia that are also subepidermal, slightly columnar, containing catenate teliospores with lateral coalescence, later becoming pulverulent and germinating away at the apex. In *Kuehneola,* on the other hand, the urediospores are stipitate and the telia consist of catenate teliospores but the chains remain free right up to the base.

The rust on *Heterophragma Roxburghii* has the characters mentioned above for the genus *Cerotelium* so far as the structure of the telium and the type of germination are concerned. But when the other spore-forms are taken into consideration, differences begin to manifest themselves. The pycnia are no doubt subcuticular both in *Cerotelium* and the present rust but the lack of ostiolar filaments is stressed as an important character for *Cerotelium* whereas they are quite conspicuous in the present rust. The aecia are cupulate and peridiate *Cerotelium Dicentrae* (Trelease) Mains who first (**1921**) described the aecial stage for the genus, whereas they are subcuticular and uredinoid in the *Heterophragma*-rust. The lack of a peridium or hyphoid paraphyses in

the uredia, as well as the pedicellate nature of the urediospores of the latter rust, indicates that the rust belongs to a separate genus. Subepidermal crusts of telia with teliospores developing in chains are known in *Angiopsora, Dasturella* and the rather imperfectly known Bignoniaceous rust *Uropeltis*. The genus *Angiopsora* is separated from *Phakopsora* only in having teliospores in chains. But in both the genera the telia are non-erumpent and the teliospores are resting spores. In *Dasturella,* which has erumpent telia, they are in the form of flabelliform crusts and the teliospores are also resting spores and do not germinate as soon as they mature as in the *Heterophragma*-rust. The combination of characters found in this rust necessitates therefore the erection of a separate genus for its accommodation. The name *Santapauella,* for Rev. Father Santapau, is proposed for it.

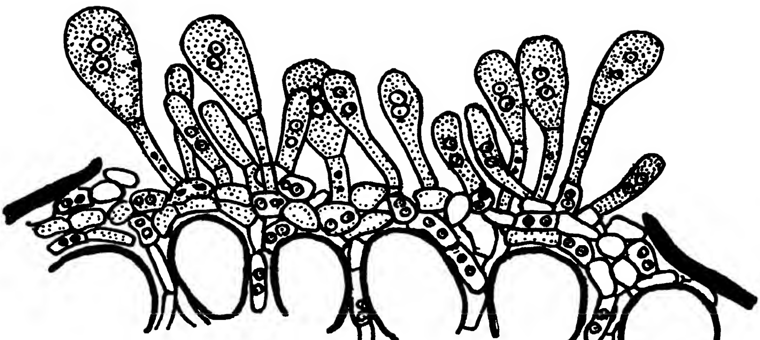
The genera *Mehtamyces* and *Santapauella* can be differentiated among themselves on the basis of the following characters. In both the uredia are subepidermal but the urediospores are borne in clusters on sporogenous basal cells in the former and singly on pedicels in the latter. The hyaline hygroscopic sheath forming the outer layer in both the genera is reminiscent of *Prospodium* but the apex is bicapitate in *Mehtamyces* and unicapitate in *Santapauella*. In *Mehtamyces* the telia are not erumpent, and the teliospores which are formed as crusts within the leaf tissue are resting spores. As against this, in *Santapauella* the telia are erumpent, develop as short columnar crusts and tend to become pulverulent and germinate away at the apex as soon as they are mature.

Santapauella gen. nov.

Pycnia subcuticular; aecia uredinoid, subcuticular and aparaphysate; uredia suberpidermal, aparaphysate, with pedicellate spores borne singly on pedicels; telia in subepidermal crusts, erumpent, pulverulent at apex; teliospores catenate, hyaline, germinate without a rest period.

Type species: *Santapauella Heterophragmae* Mundkur & Thirumalachar.

Pycnia subcuticularia. Aecia uredinoidea, subcuticularia, aparaphysata. Uredia subepidermalia, aparaphysata, ornata, sporis pedicellatis, quarum



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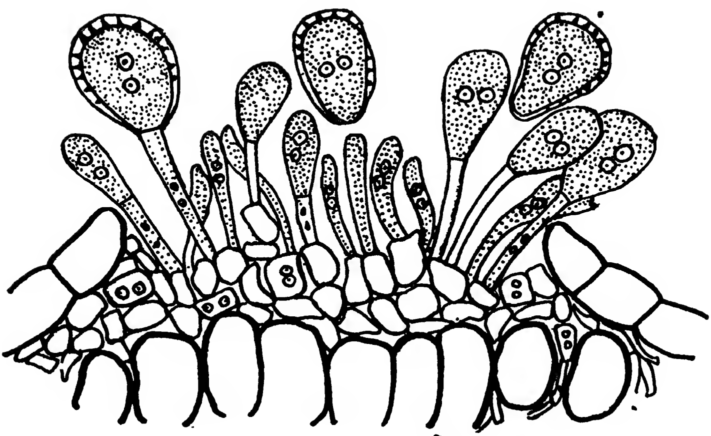

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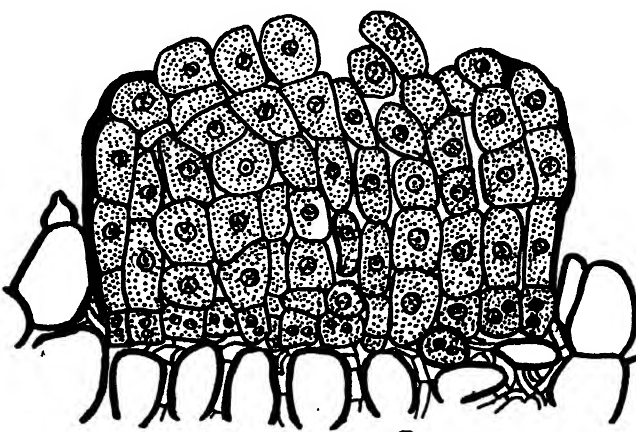

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FIGS. 6–8. *Santapauella Heterophragmae.*

singulae pediculo insident. Telia in crustis subepidermalibus, hyalinae, germinantes absque ulla quietis mora.

Species typica: *Santapuella Heterophragmae* Mundkur & Thirumalachar.

Santapauella Heterophragmae sp. nov.

Pycnia conoid, broader than long, sometimes compressed, with ostiolar paraphyses 220 to 330 μ broad and 100–155 μ high; pycniospores hyaline to pale yellow. Aecia erumpent, indefinite because of coalescence; aeciospores resembling urediospores, measuring 24–32.5 × 20–27 μ. Uredia amphigenous, erumpent, pulverulent; urediospores, borne singly on pedicels, obovate to ellipsoid, sparsely echinulate, measuring 24–32 × 20–27 μ; with three approximately equatorial germ pores; wall bilaminate, inner golden yellow up to 5 μ thick; outer hyaline, hygroscopic, forming a band on one side, appearing to be unicapitate. Telia amphigenous, aparaphysate; teliospores in chains with 7 to 10 spores per chain, chains coalescing laterally, hyaline to pale cinnamon yellow, smooth, without distinct pores at maturity, measuring 11–19 × 9–17 μ; germination as soon as teliospores are mature, starting at apex.

On living leaves of *Heterophragma Roxburghii* DC. Khandala (Bombay), 13–6–1943, coll. H. Santapau (No. 2207); Lalbagh, Bangalore (Mysore), 8th September, 1944, coll. M. J. Thirumalachar & B. B. Mundkur (type); deposited in the Herb. Crypt. Ind. Orient.

Santapauella Heterophragmae sp. nov.

Pycnia conoidea, latitudine praestantiora quam longitudine, nonnumquam compressa filamentis ostiolaribus; pycniosporae hyalinae ad pallide luteas. Aecia erumpentia, ob coalescentiam indefinita; aecisporae urediosporis similes, magnitud. 24–32.5 × 20–27 μ. Uredia amphigena, erumpentia, pulverulenta; urediosporae singulae pediculis insidentes, obovatae ad ellipsoideas, sparse echinulatae, magnit. 24–32 × 20–27 μ; tribus germinationis poris plus minus equatorialibus ornatae; parietes duplices, quorum interior luteus, ad 5 μ crassus; exterior hyalinus, hygroscopicus, vittam in latere efformans atque unicapitatus apparens. Telia amphigena, aparaphysata; teliosporae catenatim dispositae (7–10 sporis in singulis catenis, quae lateraliter coalescunt), hyalinae ad cinnamomo-luteas, leves, absque distinctis germinationis poris in maturitate, magnitud. 11–19 × 9–17 μ; germinant statim ac teliosporae ad maturitatem perveniunt, ab apice incipientes.

In foliis viventibus Heterophragmae Roxburghii DC. Khandala (Bombay), 13–6–1943, legit H. Santapau; Bangalore (Mysore), 8–9–1944, leg. M. J. Thirumalachar et B. B. Mundkur (typus).

We wish to express our deep debt of gratitude to Rev. Father Santapau for his kindness in placing at our disposal his collection of rust on *Heterophragma Roxburghii* and for rendering into Latin the diagnoses of the new genera and species and to Dr. G. B. Cummins for drawing our attention to some of the salient points in the life history of the above rusts.

HERB. CRYPT. IND. ORIENT.,
IMPERIAL AGRICULTURAL RESEARCH INSTITUTE,
NEW DELHI, INDIA, AND
BOTANY DEPARTMENT, CENTRAL COLLEGE,
UNIVERSITY OF MYSORE, BANGALORE,
INDIA

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EXPLANATION OF FIGURES

Mehtamyces Stereospermi

1. Section through the telium showing development between epidermis and palisade layers. × 400.
2. Enlarged view showing chains. × 900.
3. Mature teliospores. × 1020.

Santapauella Heterophragmae

4. Subcuticular pycnium. × 720.
5. Urediospore showing bilaminate wall and germ pores. × 900.
6. Uredinoid aecium. × 400.
7. Uredium. × 400.
8. Telium showing erumpent columns. × 400.

FURTHER REMARKS ON MYCOGENETIC TERMINOLOGY

B. O. Dodge

HETEROCARYOSIS AND HETEROSIS

When race "yellow dwarf 16" of *Neurospora tetrasperma* was grown in "mixed culture" with race C_4, nuclear migrations occurred so that a heterocaryotic mycelium was soon built up (Dodge, **1942**). This mycelium then grew with great vigor. It was pointed out that we had here a phenomenon analogous to hybrid vigor in diploid plants and animals. Since a heterocaryotic haploid mycelium is in no sense hybrid, the phrase heterocaryotic vigor was suggested to characterize the phenomenon. One frequently finds in recent literature statements such as "hybrid vigor or heterosis," implying that the two expressions are synonymous. Whaley (**1944**), however, has reminded us that this is an erroneous use of the term heterosis since Shull (**1914**) defined it as the "stimulus of heterozygosis," the "stimulating effects of hybridity" or "the stimulation due to the differences in uniting gametes." According to Shull, then, hybrid vigor is the *manifestation* of the effects of heterosis which in turn is the *stimulus* of heterozygosis. All three terms apply to diploid organisms, although those having more than the 2n number of chromosomes might very well show hybrid vigor, that is, if they are heterotic hybrids.

It is obvious that it would be incorrect to say that heterocaryotic vigor is one form of heterosis. Hanson and Smith (**1932**) were fully aware that dicaryotic and heterocaryotic mycelia are not hybrid diploid structures when they first suggested the term "heterocaryosis" to cover situations where two or more genetically different kinds of nuclei are operating in the same cells or in the same cytoplasm. Heterocaryosis should be compared to heterozygosis and not to heterosis. There is at present no mycogenetic

term comparable to heterosis. One can say, however, that heterocaryotic vigor is the manifestation or the effects of the stimulus of heterocaryosis. At the time when Shull (**1914**) defined "heterosis" the phenomenon heterocaryotic vigor had not been recognized as such. From conversations and correspondence with that author we must believe that had this phenomenon been known he would have broadened his concept of heterosis to include stimuli of heterocaryosis.

The writer's associates Dr. W. J. Robbins and Dr. H. W. Rickett on being approached on this point suggested that the word "choriheterosis" could be used to signify the stimulus of heterocaryosis, and "synheterosis" to signify the stimulus of heterozygosis. The following chart may serve to bring out the relationship of two comparable sets of terms.

Haploid organisms	Diploid organisms
1.[1] Heterocaryotic vigor	1a. Hybrid vigor
(Heterosis)	
2. Choriheterosis	2a. Synheterosis
3. Heterocaryosis	3a. Heterozygosis

[1] Nos. 1 and 1a refer to manifestations;
Nos. 2 and 2a refer to stimuli;
Nos. 3 and 3a refer to spatial or organic relationships of the genes involved.

There would be no point in using the term heterosis, as some have done, to mean hybrid vigor which is such an expressive phrase and one that can not be improved upon. Much has been written on the causes of hybrid vigor and the stimulus of hybridity. If an equal amount of research by equally well equipped investigators were devoted to heterocaryotic vigor and the effects of heterocaryosis we might come to a better understanding of hybrid vigor. For this work the facultatively heterothallic ascomycetes such as *Neurospora tetrasperma* would serve most admirably.

HETEROTHALLISM AND HAPLODIOECISM

It was not possible to include in a recent note on terminology (**Dodge, 1945**) an extended discussion of heterothallism. Jackson

(**1944**) made the very good point that Blakeslee's (**1904**, **1906**) definition of this term carried with it "a definite implication with reference to the separation of the sexes in different thalli." When one reads only those two papers one must agree with Jackson, especially in view of the fact that in plate 6 (Blakeslee, **1906**) the symbols ♀, ⚥ and ♂ were used exclusively instead of the symbols + and −. Certainly it does look as though femaleness and maleness were uppermost in his mind, plus (+) being female and minus (−) being male. Even in some of his later papers the same idea was more or less emphasized, but more from the biochemical standpoint. However, if one rereads all his papers on sex one must be convinced that we have not gradually come to apply the terms heterothallism and homothallism in an entirely different way from that which their author intended forty years ago.

Heterothallism does imply the segregation of factors which control sex-reactions or which determine mating types. It is genotypic and does not imply phenotypic, morphological sex-differentiations. An example will be cited later showing that rarely the two types of differentiation may possibly operate in a closely linked fashion.

Blakeslee's "type material" which served as the basis for his new term heterothallism was, no doubt, the "Harvard strain" of *Rhizopus nigricans*. This he found, to the consternation of many conservative teachers of botany, was really a mixture of two different strains, neither of which could produce zygospores by itself. Individual spores from a sporangium were not totipotent. There were no constant differences morphologically between the two progametangia which united to form zygospores in fertile cultures. Nevertheless, the two races which united to bring about sexual reproduction were genotypically of opposite sex. All heterothallic species of the Mucoraceae are like *Rhizopus* in the three respects circumscribing heterothallism, as noted above. Haplodioecism should, as other authors have pointed out, be reserved for those haploid organisms which do have two kinds of thalli, "male" and "female" thalli which can be distinguished morphologically. A few quotations from Blakeslee's papers support the above conclusions.

He says (**1906**, p. 163), "That as yet it has not been possible to substitute the terms male and female for (+) and (−) or *vice versa*, does not in the least detract from the conclusion, however, that the differentiation is a sexual one." Page 175 of the same paper, he says, "A heterothallic condition on the other hand can never be recognized by a morphological investigation alone."

In his retiring Vice-presidential address Blakeslee (**1920**, p. 377) says also, "In a considerable number of races in several species, however, I have found that the plus race is not invariably more vigorous than the minus when a difference in vegetative vigor is observed, judging vigor by former criteria; but this fact does not detract in the least from the evidence that in the plus and minus races we have two sexes represented." Farther on, "The main point to be brought out is that dioecious mucors are not to be homologized with dioecious flowering plants and higher animals. More nearly are the sexual races of mucors to be compared with the gametes themselves of such higher plants and animals." Notice he says in the last sentence *"more nearly"* and not "exactly"! In the same address he says of the sex reactions of *Zygorhynchus heterogamus*, "they serve to call attention to the fact that those who define male and female in terms of size differentiation in sex cells are making the gratuitous assumption that quantitative differences in the gametes are the fundamental peculiarities of the two sexes. I have used from preference, therefore, the terms plus and minus because I wish to speak in terms of physiological differentiation into sexually dimorphic races established in dioecious species rather than in terms of male and female which are defined by differentiation in size of gametes and which conceivably may be secondary sex characters."

In certain species of the Florideae the thalli are of two sorts, carpogonial and antheridial. Such thalli are often referred to as female and male plants. Many red algae are bisexual or hermaphroditic. It is strange that Blakeslee should have failed to cite such examples if he really had this type of femaleness and maleness in mind when he defined heterothallism and referred to the thalli of opposite sex as + and − thalli.

Much more to the point is his omission of the haplodioecious species of the Laboulbeniales. Working in close association with

Thaxter who described a dozen or so "dioecious" genera with numerous species, Blakeslee must have known all about them, at least by 1920 when he gave us his mature judgment on the nature of heterothallism, and specifically insisted that heterothallism can never be recognized by a morphological study alone. The writer (**1927**) stretched the point considerably when he stated that we should call those species of *Dioicomyces*, for example, heterothallic and not dioecious. Thaxter (**1931**) adopted this suggestion. In his table of contents he listed the genera to be treated under "heterothallic" and "homothallic." Discussing *Apatomyces* (p. 79) he used the expression "unisexuality or heterothallism." To-day it would seem to the writer to be more in accord with Blakeslee's definitions to refer to Thaxter's "dioecious" species as haplodioecious and not as heterothallic, and to his "monoecious" species as haplomonoecious and not as homothallic. Thaxter fully recognized that haplodioecious differences might well be a provision for preventing self-fertilization. He also pointed out that cross fertilizations in "monoecious" species may very well be the more frequent because the antheridia mature earlier than the carpogonia on the same plant. "Antherozoids" mature on the plant over long periods after its carpogonia have been fertilized. Haplodioecious red algae and Laboulbeniales species certainly could also be heterothallic in the Blakeslee sense, but no one has as yet proved this experimentally.

We have in *Ascobolus magnificus* (Dodge, **1920**) a species which may possibly be both haplodioecious as well as heterothallic. Thalli from single ascospores produce neither ascogonia nor antheridia when grown separately. It is only when two thalli of opposite sex-reaction are grown together that very striking ascogonia and antheridia develop. They are, however, always formed on *different* hyphal branches. Shear and Dodge (**1927**) discussing this *Ascobolus* say: "In all probability the gametophytes come to maturity and produce reproductive structures only when grown together in the same medium, the mycelium of each sex so changing the nature of the medium as to stimulate the development of the reproductive structures on the mycelium of the opposite sex." We know that *Ascobolus magnificus* is heterothallic but we do not know whether it is haplomonoecious or haplodioecious.

Raper (1940, 1942) has described some highly interesting experiments with species of *Achlya,* which when fully supplemented with genetic experiments will really show how complicated can be the questions of sex, sexuality, phenotypic sex cell-differentiations, heterothallism, haplodioecism, homothallism and haplomonoecism. Those who seek to explain everything relating to sex in the fungi by some simple formula should read Raper's very illuminating papers. He has shown, first of all, that there must be factors, no doubt heritable and segregated at meiosis, which govern the synthesis of sex stuffs, just as must be the case with *Ascobolus magnificus.* In both instances the effects of these sex hormones are manifested by the development of sex organs. It is not clear, however, whether or not other heritable factors in addition to those readily manifested, are a necessary adjunct. Are heterothallism and haplodioecism synonymous in *Achlya?* Are those sex factors which determine the +/− relations ever the same ones that govern the differentiation of the ♀ and ♂ sex organs? We must await adequate genetic work on such forms as *Ascobolus magnificus* and the species of *Achlya* before these questions can be settled. Raper, in his discussions, appears to be cognizant of the complexity of the situation as he does not make too many sweeping statements one way or another. We are not quite clear, however, as to his latest views on what constitutes heterothallism in *Achlya bisexualis* and *A. ambisexualis.* In the syntheses of sex stuffs by races of opposite mating types, *Achlya* and the species of *Chlamydomonas* worked on by Moewus (1938) have something very important in common.

Species of *Neurospora* (Shear and Dodge, 1927), *Sclerotinia gladioli* (Drayton, 1932) and *Bombardia lunata* (Zickler, 1934) are excellent examples of heterothallic species of the sort in which, theoretically at least, mycelia from single ascospores often produce both incipient ascocarps and spermatia. They are of the class which we should refer to as normally haplomonoecious *and* heterothallic. The fact that certain races fail to produce ascogonia or other receptive structures, and that other races fail to produce spermatia, does not alter the fact that production of ascocarps by heterothallic species is regulated first of all by pairs of factors primarily concerned with sex-reactions or mating type differences such as Blakeslee would characterize as +/− relationships.

Aronescu (**1933**) found a rather well-marked segregation of factors controlling the development of incipient perithecia. When a certain pair of albinistic races of *Neurospora sitophila* were crossed, four of the progeny races from single asci developed large numbers of "sclerotia" (incipient perithecia). These cultures were dark grayish in appearance. The other four f_1 races produced few if any incipient perithecial primordia; on Czapek's medium no incipient perithecia were formed. To be on the safe side she concluded merely that while she obtained a clear cut segregation of factors controlling abundance and paucity of perithecial primordia, one should interpret her results as showing merely that some races are capable of greater fructification than others as indicated by their numbers of receptive bodies.

Zickler (**1934**) reported important genetic work on *Bombardia lunata*. His figures of ascogonia and spermatangia with spermatia leave little to be desired as proving that normally a mycelium from a single ascospore is haplomonoecious. The species is also strictly heterothallic. He refers to the two kinds of thalli as *A* & *a* reaction groups. Among other things he found both *A* races and *a* races of *"bulbosa,"* both normally producing a great many incipient perithecia and also spermatia. Another race, *"lanata,"* produced few if any incipient perithecia although this race always produced many spermatia. Segregations were such that he obtained *"lan"* races which were of opposite sex-reaction types, *A-lan* and *a-lan*. Now when he attempted to intercross these four races by the spermatization method he obtained the results which were indicated in his diagram. The solid lines indicate positive reactions resulting in normal perithecia; broken lines indicate failure.

It is self-evident that if a mycelium does not develop perithecial primordia or receptive structures, either by itself or under the stimulus of spermatization or of sex-hormones, it can not be made to fructify. Zickler says that from his diagram one might get the impression that he had here something comparable to the tetrapolar type of segregation such as prevails in certain higher basidiomycetes. This he says is not the case, however.

(*To be concluded*)

NOTES AND BRIEF ARTICLES

Common Names May Be Highly Important

One is accustomed to think of common names as merely incidental, to be changed at will. Not so with the common names of poisonous plants, however. A single instance will illustrate what I mean.

Krieger did an excellent job in his "Guide to Mushrooms." There is almost nothing to criticize in all the fact-filled 500 pages. But in selecting a common name for *Amanita verna* he translated the Latin and used "Spring Amanita," a procedure followed in thousands of cases and ordinarily perfectly legitimate. Then he came to *A. virosa,* which had no common name, so he called it "Destroying Angel." It is white, it is deadly—what's wrong with the name? Simply this; it belongs to another plant (*A. verna*) and the arbitrary change, while perfectly innocent, might lead to endless confusion and possibly serious consequences.

W. A. Murrill

A New Name

Since the generic name *Longia* has already been applied to a genus of rusts by Sydow [1] the use of the same name for a genus in the Gasteromycetes is untenable.[2] The generic name **Longula** gen. nov. will therefore apply to this genus of Gasteromycetes and the combinations will be **Longula texensis** (Berk. & Curt.) Zeller comb. nov., and **L. texensis** var. **major** Zeller comb. nov.

S. M. Zeller

A Simple Method for Preparing Corn Meal Agar

In identifying various yeast-like fungi isolated from human sources, one has recourse to the use of corn meal agar.

[1] Ann. Myc. **19**: 165. 1921.
[2] Zeller, S. M. Mycologia **35**: 414–417. 1943.

The usual methods cited for the preparation of this agar call for several filtrations through paper and cotton. These operations are quite tedious. With the use of a "Silex" type coffee pot fitted with a "Cory glass filter rod," it has been found practicable to prepare the agar in less time and with greater simplicity.

The technique is the same used in brewing coffee except that 40 gm. of yellow corn meal are used in place of the ground coffee and 500 ml. of distilled water in place of tap water. The water is then heated and passed and repassed through the corn meal not once but at least eight times. At the end of this procedure, the volume of the extract is measured, brought back to 500 ml., and the extract then added to a two liter flask containing 15 gm. of agar and 500 ml. of distilled water. The flask is plugged and autoclaved for 15 minutes at 15 pounds pressure. Plates can then be poured and stored away till needed.

LIBERO AJELLO, Mycologist

OFFICE OF SCIENTIFIC RESEARCH AND DEVELOPMENT,
THE JOHNS HOPKINS HOSPITAL,
BALTIMORE 5, MARYLAND

THE RELATION BETWEEN VERMICULARIA GRAMINICOLA WEST. REPORTED ON SUGARCANE AND PHYSALOSPORA TUCUMANENSIS SPEG.

In 1896 C. Spegazzini [1] reported *Vermicularia graminicola* West. as occurring upon sugarcane leaves (*Saccharum officinarum*) in Argentina. Material of this was obtained from Juan C. Lindquist of the "Instituto Spegazzini," La Plata, labeled "No. 6750." After careful microscopic examination of this material, it was found that it contained two different types of fruit bodies, acervuli and perithecia. The conidial stage represented by the acervuli (conidia, setae, and appressoria) fit the description of *Colletotrichum falcatum* Went, while the perithecial or ascosporic stage was typical of *Physalospora tucumanensis* Speg.

The conidial and perithecial stages found in Spegazzini's material agreed reasonably well with those of the red rot fungus of

[1] Spegazzini, C. Hongos de la cana de azucar. Rev. Fac. Agron. y Vet. **2**: 227–258. 1896.

sugarcane as studied by the writer [2] in Louisiana. Therefore, it is considered that Spegazzini's specimen of *Vermicularia graminicola* is cospecific with *Physalospora tucumanensis*. This Argentinian material has been kept in the herbarium of the Botany Department at Louisiana State University, Baton Rouge, Louisiana, under the number 4667 as *Physalospora tucumanensis* Speg.

FERNANDO CARVAJAL

LAWRENCEBURG, INDIANA

SELENOPHOMA ON GRASSES, II [1]

Maire (Bul. Soc. Bot. Fr. **53**: CLXXXVII. 1906) described the genus *Selenophoma* as follows:

> *"Conceptaculis immersis, erumpentibus vel subsuperficialibus, ostiolo punctiformi plus minusve papillato, membranaceis, nigris; sporis* Vermiculariae *quasi curvatis et utrinque acutis, muticis, hyalinis; sporophoris brevissimis simplicibus."*

This genus is hereby emended to include also species with somewhat obtusely pointed spores, other characters agreeing. With this emendation, the following new species is described.

Selenophoma obtusa sp. nov.

Maculis fulvellis, margine fusco v. lavendulo; pycnidiis globosis, nigris, 40–150 × 40–138 μ; pycnophoris cuspidatis, prominulis, 3–7 × 2–3.5 μ; pycnosporulis curvatis, utrinque obtusis v. sub-acutis, 13–17 × 2.5–4.2 μ. Hab. in foliis et culmis vivis *Sitanii hystricis*, Mt. Shasta, Calif. (typus), *S. Hanseni, Stipae Richardsonii, Poae aridae, Elymi glauci, E. condensati*, et *Agropyri inermis* in America Boreali occidentali.

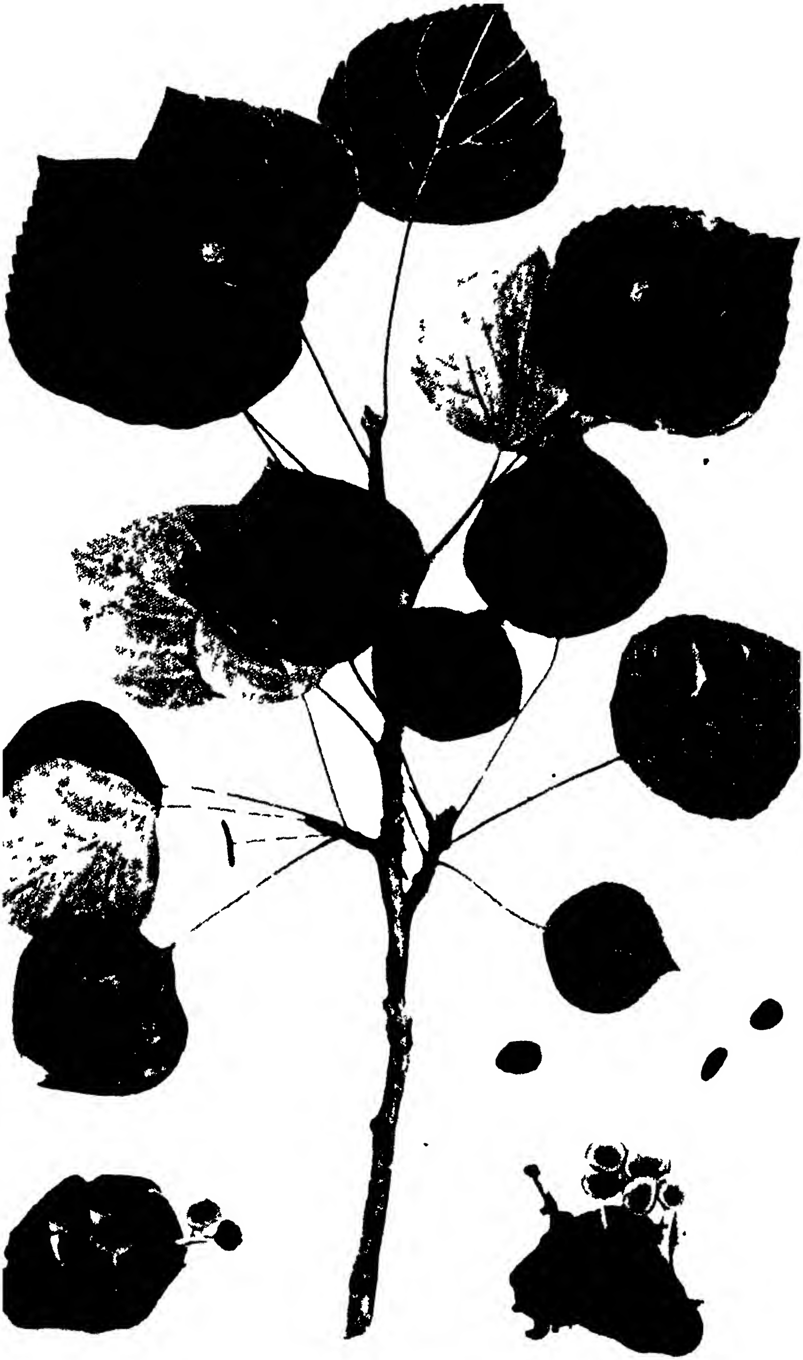
[2] Carvajál, Fernando & Edgerton, C. W. The perfect stage of *Colletotrichum falcatum*. Phytopath. **34**: 206–213. 1944.

[1] (Selenophoma on Grasses, [I], Mycologia **32**: 415. 1940.) Coöperative investigations between the Divisions of Cereal Crops and Diseases, Forage Crops and Diseases and Dry Land Agriculture, Bureau of Plant Industry, Soils, and Agricultural Engineering; and Nursery Division, Soil Conservation Service, U. S. Department of Agriculture and the Oregon and North Dakota Agriculture Experiment Stations.

Published with the approval of the Director of the Oregon Agricultural Experiment Station as Technical Paper No. 471, contribution from Department of Plant Pathology.

It is proposed also that *Phyllosticta stomaticola* Bauml. be included in *Selenophoma Donacis* (Pass.) Sprague and A. G. Johnson as **S. Donacis** var. **stomaticola** (Bauml.) comb. nov. Also that *Septoria Everhartii* Sacc. & Syd. be transferred to the genus *Selenophoma* as **S. Everhartii** (Sacc. & Syd.) comb. nov.

RODERICK SPRAGUE AND A. G. JOHNSON



SCLEROTINIA BIFRONS

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SCLEROTINIA BIFRONS

FRED J. SEAVER

(WITH 2 FIGURES)

The report of the perfect stage of *Sclerotium bifrons* from material collected in Colorado in 1929, while on a collecting trip with Dr. Paul F. Shope of the University of Colorado,[1] has caused considerable discussion and given rise to much misunderstanding. The following notes were prepared in 1940 in reply to an article by our late friend and colleague H. H. Whetzel.[2] It is regretted that they could not have been published during his lifetime, but since all points have been freely and sometimes "heatedly" discussed with him, the writer has no misgivings in presenting them now, hoping that they may correct some of the misinformation given out regarding our Colorado fungus. The fungus in question was collected near the University of Colorado summer camp after a special search for the perfect stage of the poplar sclerotium.

In a ravine[3] not far from the camp, in as pure a stand of *Populus tremuloides* as could be found, and where the trees were at the time loaded with the sclerotia of *Sclerotium bifrons,* we finally succeeded in locating sclerotia on the ground producing a perfect stage in great abundance. Hundreds of sclerotia, each with a

[1] MYCOLOGIA 22: 3, 1930.

[2] MYCOLOGIA 32: 124–127, 1940.

[3] A ravine was selected since the conditions of moisture seemed more favorable for the growth of the fungus if it did occur.

[MYCOLOGIA for September–October (37: 527–639) was issued October 1, 1945]

clump of stalked fruiting bodies, were collected. The ascomycete was active and the minute apothecia puffing spores like miniature steam engines, although it was late in the month of July. In our account of the trip this was reported as the perfect stage of *Sclerotium bifrons* under the name of *Sclerotinia bifrons.* It was later observed under other stands of poplars in that general region.

In the meantime we learned that Professor Whetzel had been collecting the perfect stage of *Sclerotium bifrons* in the East and, knowing that he was working on the group, Colorado material was transmitted to him for study. Comparison by Whetzel soon revealed the fact that we had not one but two species on what had been regarded as *Sclerotium bifrons.* Immediately Whetzel assumed that his was the orthodox perfect stage of *Sclerotium bifrons,* and the fungus reported by us as such was an "imposter."

In an attempt to discredit our observations, two lines of argument were adopted by him. First he claimed that our fungus was not a *Sclerotinia,* but a *Helotium* growing on *Sclerotium bifrons.* This could have been possible, but was scarcely likely. Later he abandoned this line and conceded that what we had from Colorado was a *Sclerotinia,* but that it did not come from the poplar *Sclerotium bifrons.* Just what it did come from he did not know. All this argument was purely academic since he had never collected in Colorado.

I might illustrate Whetzel's course of reasoning in the following manner: If one should go out into an apple orchard and find a crabapple tree loaded with a certain kind of crabapples, and at the same time find numerous "free lying" apples of the same kind under the tree, he would naturally assume that the apples on the ground came from the branches overhead. If his friend, who had not visited this orchard, should argue that the apples on the ground did not come from the tree under which they were found, but from some other tree, although no other tree was known to produce this kind of apple, and from such other place, he did not know where, and that they were transported to this particular apple tree by some unknown agent, he did not know what, the argument would be too "far fetched" and ridiculous to even merit serious consideration. Yet this is exactly the line advanced by Whetzel in his determined effort to discredit the field observations of Dr. Shope and myself,

since these observations seemed to conflict with his own made in the East.

If Whetzel had worked as hard to explain our observations made in Colorado, as he did in his futile attempt to disprove them, without any first-hand field observations, he would have had no difficulty in concluding that there was no incompatibility between these two claims, but that in reality we have two species of *Sclerotinia*, both occurring on what was supposed to be the same sclerotium on the same host. This might be accounted for in the following manner:

Populus tremuloides as it occurs in the Rocky Mountain region is regarded by botanists here as a distinct variety from that occurring in the East. Therefore, *Sclerotium bifrons* of the Rocky Mountain variety of *Populus tremuloides,* while to all outward appearances identical with the eastern form, and so regarded by Ellis himself, is in reality different, these differences so far as observed to date manifesting themselves only in the perfect stage. On this assumption, our apothecial stage collected in Colorado is the perfect stage of the Rocky Mountain form of *Sclerotium bifrons,* while those collected in this region (New York) are the perfect stage of the Eastern form of the same species. From this we would conclude that what has been regarded as *Sclerotium bifrons* by various mycologists, including Ellis himself, really represents not one but two, and possibly several distinct species. A similar situation has been reported by Drayton [4] and others, where three distinct species of *Sclerotinia* have been connected with what has commonly passed as *Botrytis cinerea* as their conidial stage. Whether the species on poplar can be distinguished in the sclerotial stage remains to be seen, but it is quite evident, as Whetzel has pointed out, that in their perfect stages they are two very different species.

Another bit of evidence advanced by Whetzel to prove that our Western species is not *Sclerotinia bifrons,* is the fact that according to his records *Sclerotinia bifrons,* as he knows it in the East, discharges its spores over a period of ten days to two weeks during the time when the leaf buds are bursting and the young leaves unfolding, which would be about April or May, while the plants of

[4] MYCOLOGIA 31: 485–489, 1939.

our species reported from Colorado were found shooting their spores vigorously late in July. Here again Whetzel is comparing the behavior of two different species. It must be borne in mind that even the same species of fungi do not behave in the same manner at an elevation of 9,600 feet that they do a few hundred feet above sea level. The writer has often observed high in the Rocky Mountains in August species of fungi which would be known in this locality (New York) only in early spring. Consequently, we would expect that a high altitude species of *Sclerotinia* would not mature and discharge its spores at the same season of the year that a low altitude form of the same genus might do.

The writer has not had a chance to study the Colorado species in the field over a long period of years, as Whetzel has the Eastern form, and is therefore unable to furnish all the details as to time and manner of host infection and length of fruiting period, as could be done if we lived in the region where this species occurs. Doubtless this will be done at some time, by some local student, and the story will be made complete.

Still another point frequently raised by Whetzel, and emphasized in his paper, is the fact that our species in Colorado occurs "On the ground from *free lying* sclerotia entangled in leaf debris, under trees of *Populus tremuloides,*" and that the sclerotia were never found producing apothecia while attached to the leaf on which they were said to be produced. This may be explained by the fact that the sclerotia when mature drop out of the leaf and fall to the ground unattached, although many do also fall with the leaves. Whether those that fall with the leaves are sufficiently mature to produce apothecia is not known, but if they do the leaf tissues are pretty thoroughly disintegrated. In order to show the way in which the sclerotia do dehisce from the leaves, the writer is offering in evidence a photograph (FIG. 2) of the leaves taken in the Rocky Mountains, which are apparently full of shot holes where the sclerotia have been released. This will account for the production of apothecia on "free lying" sclerotia. Whether the apothecia are produced the following season after the sclerotia are released, or later, we have no means of knowing.

The reader is asked to note carefully the variation in the form of the shot holes after the dehiscence of the sclerotia, especially

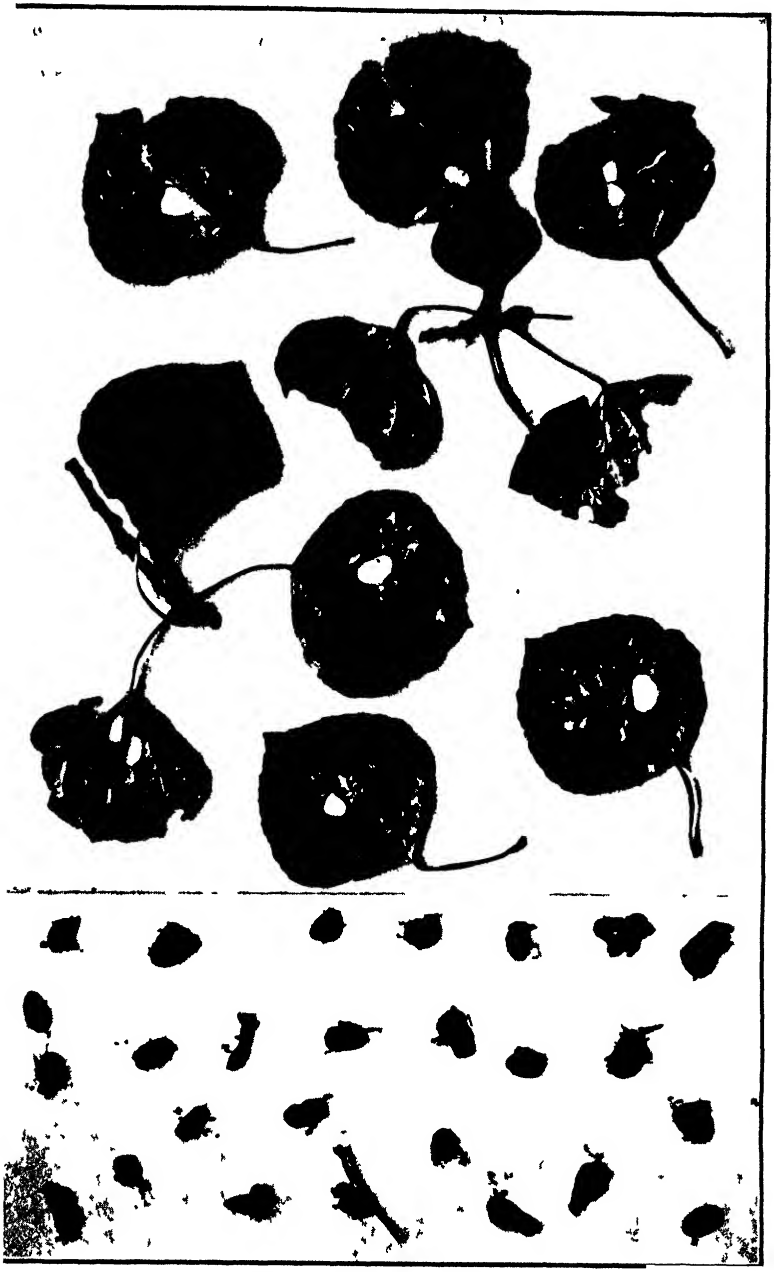


FIG. 2. *Sclerotinia bifrons.*

the tendency to assume a semi-triangular form with rounded corners. The reader is then again asked to compare these with the free-lying, apothecia-producing sclerotia, bearing in mind that these are photographs and not drawings (FIG. 2). So far as size is concerned, there is no discrepancy between size of the holes and sclerotia which are reported to have come from them. The resemblance in size and form of those on the ground and those on the tree is alone evidence that the apothecia-producing sclerotia did come from the poplar leaves, if we needed any further evidence. The origin of the sclerotia was so obvious to us working in the field in Colorado that no such extraneous evidence is necessary, but is cited here for the benefit of those who have not had the privilege of seeing the fungus in the field, and who might be misled by arguments advanced to disprove our observations.

Perhaps the most striking piece of evidence advanced by Whetzel is his announced discovery in the debris accompanying specimens of our fungus sent him from Colorado of foliar remnants of some other plant than the poplar. He immediately assumes that this unknown plant "may represent the real suscept" of our *Sclerotinia*. He does not know what the plant is since no other in the Rocky Mountains is known to produce this particular type of sclerotium. Neither does he explain how these fruiting sclerotia came to be accumulated in such large numbers under poplar trees which were seen to be producing the same type of sclerotia at the same time, nor why they were not found in any other situation during our summer's work in the West. Such minor details are lightly brushed aside.

Having thus thoroughly convinced himself that the poplar *Sclerotinia* reported by us is not of poplar origin at all, and knowing that his *Sclerotinia* in the East is, he feels perfectly justified in taking over the name applied to our fungus ten years earlier and applying it to his own, and recording our fungus as a new species of his own under the name *Sclerotinia confundens* Whetzel. Misdetermination of host is no valid ground for changing the name of a fungus, even if proven. In this case not one shred of real evidence has been advanced to disprove our claim or to substantiate his own. To attempt to change a name on mere suspicion of error is not only illegal but inexcusable.

SUMMARY

The specific name *confundens* is untenable since the fungus described as "*Sclerotinia confundens* Whetzel sp. nov." in 1940 had been previously recorded under the name *Sclerotinia bifrons* Seaver & Shope in 1930, and reported as the ascigerous stage of *Sclerotium bifrons* from poplar trees in Colorado. Whetzel's claim (MYCOLOGIA **32**: 125) that the Seaver and Shope report was based on an "error in identification," apparently referring to the fungous host, was absolutely groundless and unjustified, but, even if true, would furnish no valid reason for the rejection of the Seaver and Shope binomial and the redescription of their plant as a new species ten years later under a different name, and finally applying the rejected binomial to another plant thus establishing a homonym which could have no legal standing and which under the International Rules **must** be rejected. Obviously *Sclerotium bifrons* on poplars like the so-called *Botrytis cinerea* has more than one ascigerous stage. The synonymy of the two species on poplar sclerotia would then be as follows:

1. SCLEROTINIA BIFRONS Seaver & Shope, 1930 (Not *Sclerotinia bifrons* Whetzel, 1940), Syn. *Sclerotinia confundens* Whetzel, 1940.
2. SCLEROTINIA WHETZELII Seaver 1940, Syn. *Sclerotinia bifrons* Whetzel, 1940 (Not *Sclerotinia bifrons* Seaver & Shope, 1930).

THE NEW YORK BOTANICAL GARDEN,
BRONX, NEW YORK CITY

EXPLANATION OF FIGURES

FIG. 1 (frontispiece). *Sclerotinia bifrons.* A branch of *Populus tremuloides* showing healthy and infected leaves. Below, photograph of three sclerotia somewhat reduced. Below, enlarged photograph of two sclerotia with apothecia. Enlarged photographs were made by Dr. Paul F. Shope from fresh material collected in Colorado. The photographs were hand colored by Fleda Griffith.

FIG. 2. *Sclerotinia bifrons.* Above, photograph of poplar showing shot-holes where the sclerotia had dropped out. Below, photograph of a number of sclerotia producing apothecia. These photographs were made from dried material.

A SYNOPSIS OF THE GENERA AND SPECIES OF THE SCLEROTINIACEAE, A FAMILY OF STROMATIC INOPERCULATE DISCOMYCETES

H. H. Whetzel[1]

(with 36 figures)

At the urgent behest of my long-time friend, the well-known mycologist, Dr. H. S. Jackson, I have been persuaded to present a synoptical view of the group of stromatic inoperculate Discomycetes with which I have busied myself at odd times during the past forty years. It is with considerable misgiving that I do so. A work of this sort had far better been left until I had completed monographs of the individual genera which comprise the family here under consideration. In spite of the fact that I have been free of teaching responsibility for the past few years, my progress with these monographs has been slow indeed. The only alibi I can offer is that I have had poor health since 1939 and have experienced the slow down which aging seems to impose. Of the fifteen genera which are here characterized I have thus far monographed but four, *Septotinia* Whetzel (**1937**), *Martinia* Whetzel (**1942**), *Lambertella* v. Höhnel (Whetzel **1943**), and *Coprotinia* Whetzel (**1944**). I have also completed a partial monograph of *Sclerotinia*, ten species of which are fully treated in "The cypericolous and juncicolous species of *Sclerotinia*," soon to appear in Farlowia. One of my former students, Dr. W. Lawrence White (**1941**), has monographed the genus *Rutstroemia*, another, Dr. Freeman Weiss, established the monotypic genus *Ovulinia* Weiss (**1940**), while a third, Dr. E. E. Honey, has in final stages of preparation a monograph of the genus *Monilinia*.

[1] Professor Whetzel died Nov. 30, 1944. This posthumous paper, unfinished at his death, was completed and submitted for publication by H. M. Fitzpatrick. See footnote 6. Financed in part by funds donated by the Mycological Society of America.

While my work on several of the other genera is well along, the rate at which these monographs have been appearing suggests that I may not live long enough to complete them all, even with the able coöperation of my students. For these reasons I commit myself to the following diagnoses of the family and genera and to assignment of species in as far as my present knowledge of these forms appears to warrant. I reserve the right, however, to repudiate any and all statements or conclusions which may later be found fallacious. I have no doubt that there are errors of omission as well as commission. It has not been possible to investigate every genus, let alone every species, with the thoroughness that such an undertaking as this requires. While I have personally studied in the living condition most of the forms here treated, I have had to rely wholly or in part on the work of others for some of them.

I am deeply indebted to so many former students and colleagues all over the world that I cannot undertake to name them. To each one who with specimens or other material contributed through the years to my studies on the stromatic inoperculate Discomycetes I here express my warmest thanks and cordial appreciation. A special grant by the Cornell trustee-faculty committee on research has greatly facilitated the preparation of this paper, and for this I am most grateful.

GROUNDS FOR ESTABLISHMENT OF THE FAMILY SCLEROTINIACEAE

The most recent attempt to provide a more satisfactory classification of the inoperculate Discomycetes is that of Nannfeldt (**1932**) in his "Studien über die Morphologie und Systematik der nichtlichenisierten inoperculaten Discomyceten." He undertakes a reorganization of the earlier systems of classification based on a study of the anatomical structure of the apothecium. That the results in many respects are far from adequate is evident in a critical examination of his work. He himself points out at various places in his paper the unsatisfactory nature of certain of his conclusions resulting from a dearth of factual knowledge and the confusion in nomenclature of certain forms. Moreover, characters other than structure of the receptacle play an important role in his attempts to delimit the families and tribes. In his order Helotiales he reduces to six the numerous families set up by earlier authors.

Whether he is fully justified in this may be debatable, but the arrangement is perhaps a more compact and convenient organization of the great mass of poorly digested observations and classifications which plague the student of the inoperculate Discomycetes, than some others that preceded it.

One of the six groups thus set up is the family Helotiaceae. Most mycologists would doubtless place in it the genera here treated, but as Nannfeldt himself points out (p. 70) it is the most heterogeneous of his six families. It is composed of clearly divergent types not clearly bound together even by his basic criterion, apothecial structure. This unsatisfactory condition is emphasized by Nannfeldt when, in undertaking to characterize this family, he remarks (p. 71) that it is easier to recognize it than to characterize it. The disunities in the family are further emphasized when one examines his attempt to bring order into these divergent forms by applying his criterion of apothecial structure to the setting up of subfamilies or tribes. He divides the family into nine tribes. The stromatic forms fall either into the Helotioideae (*e.g. Rutstroemia, Lambertella*) or the Ciborioideae (*e.g. Sclerotinia, Monilinia, Ciboria*).

Nannfeldt's description of apothecial structures in the tribe Helotioideae appears to be based entirely on his studies of *Rutstroemia firma* and five species of *Helotium*, while in the Ciboriodeae it is based on his study of but three species of *Sclerotinia*, *S. Curreyana*, *S. Vahliana*, and *S. Ficariae*. Furthermore, his contrast of apothecial structures in these two tribes does not appear to clearly distinguish them. Indeed, the number of species investigated is entirely too small. White (1941) in his studies in *Rutstroemia* shows clearly greater differences in apothecial structure among the species in that genus alone than Nannfeldt has marshalled to separate his tribes of the Helotiaceae. How little care and consideration he has given to his studies on the Ciboriodeae is indicated by his perpetuation of the old idea that the apothecia of *Ciboria Caucus* (type of the genus) do not arise from sclerotia and the erroneous concept presented by Honey (1928) of a "pseudosclerotium" in *Monilinia*. One gets the impression that while Nannfeldt's work is extensive it does not provide evidence of that intensive and detailed knowledge of species and genera

requisite for preparation of a really satisfactory system of classification of the inoperculate Discomycetes. The heterogeneous character of his Helotiaceae suggests that a more intensive and detailed study of the genera and species comprising the family might well lead to breaking it into two or more groups of family rank. The studies I have made of dozens of species commonly assigned to genera in this family lead me to the conviction that the stromatic forms constitute a fairly compact and well marked group taxonomically distinct from the non-stromatic species. The bulk of the latter appear to belong in the genus *Helotium* and related genera. When intensively studied from fresh material of all their structures they may be found to constitute another family which the name Helotiaceae would properly designate.

In the past, mycologists who have devoted attention to the classification of the Discomycetes have sought for taxonomic characters almost entirely in the apothecium, on the theory that only in the so-called "perfect stage" are reliable evidences of generic, tribal, or family relationships to be found. This is an outmoded and illogical point of view. A careful and accurate evaluation of all the structures of a fungus is necessary to a sound judgment of its place in the natural system of classification.

While the members of a natural group usually exhibit in common one outstanding character which is correlated with certain less prominent features, this is not always the case. They may exhibit their natural unity by a combination of characters no one of which is necessarily common to all of them. In the group of genera here under consideration, the development of a stroma is common to all and is the most outstanding mark of their natural relationship. Moreover, all the known species have stipitate apothecia. Certain other characters less striking help delimit the family. The typically ellipsoidal form of the ascospore is an obvious family character. The species agree in general also in the shape of the spermatium. It is chiefly globose to slightly ovate, never slender rod-shaped as it is for example in the Cenangiaceae or in certain families of the Pyrenomycetes. While stromata, stipitate apothecia, ellipsoidal ascospores, and globose spermatia are not individually peculiar to the Sclerotiniaceae, their occurrence in combination sets this group off from all other inoperculate

Discomycetes. It should be emphasized, however, that not all stromatic inoperculates belong in the Sclerotiniaceae. This is illustrated by the species of the genus *Pycnopeziza* White & Whetzel (**1938**). Their cleistocarpous ascocarp and rod-shaped spermatium exclude them and seem to relate them rather closely to the Cenangiaceae.

The designation Helotiaceae or some variant of it has been used in a slightly different sense by nearly every ambitious discosystematist since it was first started on its way by Karsten (**1871**). The group has never been clearly characterized on the basis of a comprehensive and reasonably well authenticated knowledge of the forms included. It has embraced a heterogeneous collection of genera, few of which have received detailed and critical study. The monograph of *Rutstroemia* by White, the work of Honey on the genus *Monilinia*, and the studies by the author on *Lambertella, Sclerotinia,* etc. represent a start on a critical examination of the genera commonly referred to the group.

Since apparently no previous student of the inoperculate Discomycetes has conceived of the genera here assembled as constituting a distinct family it seems desirable to designate it with a new family name. The only previous approximation to my concept of the family is the tribe *Ciboriées* in the family *Ciboriacées* of Boudier (**1907**). He, however, places the forms now regarded as species of *Rutstroemia* in his other tribe of this family, *i.e.* the *Hélotiés,* under the generic name *Phialea.* The characters on which he based his family and tribes are, moreover, quite different from those on which I here base my concept of the family Sclerotiniaceae.[2]

Family **Sclerotiniaceae** Whetzel, fam. nov.

Apothecium arising from a definite sclerotium or a stromatized portion of the substratum, stipitate, cupulate, funnel-form or saucer-shaped except in one genus where it is verpoid, *i.e.* shaped as in *Verpa,* usually brown; *ascus* inoperculate, commonly 8-spored; *ascospores* ellipsoidal, often flattened on one side, usually hyaline,

[2] The establishment of this new family under this name was first proposed by Professor Whetzel in 1943 (Lloydia **6**: 18).

unicellular and smooth; *spermatia* usually globose to slightly ovate; *conidial forms* various, in most genera lacking.

Apothecium ex sclerotio definito vel stromatita substrati parte oriundum, stipitatum, cupulatum, infundibuliforme vel patelliforme, in uno genere verpoideum, *i.e.* *Verpa*-forme, plerumque fuscum; ascus inoperculatus, plerumque octosporus; ascosporae ellipsoideae, saepe uno lato applanatae, plerumque hyalinae, unicellulares laevisque; spermatia plerumque globosa vel vix ovata; formae conideae variae, in plerisque generibus deficientes.

DESCRIPTION OF ORGANS AND DEFINITION OF TERMS

Preliminary to characterization of the genera of the family it seems desirable to describe certain organs and define certain terms as I apply them.

The STROMA is a food storage organ. The major portion of its body, constituting the MEDULLA, is wholly or partially enveloped by a rather sharply differentiated RIND. The stromata of the Sclerotiniaceae are of two generalized types, the *sclerotial* and the *substratal*. The *sclerotial stroma* (commonly called the *sclerotium*) has a more or less characteristic form and a strictly hyphal structure under the natural conditions of its development. While elements of the substrate may be embedded in its medulla they occur there only incidentally and do not constitute a part of the reserve food supply. The *substratal stroma* is of a diffuse or indefinite form, its medulla being composed of a loose hyphal weft or network permeating and preserving as a food supply a portion of the suscept or other substrate (*e.g.* culture media).

The sclerotial stromata both as to form and structure are of several more or less distinctive types which I designate here by new terms. The TUBEROID SCLEROTIA, characteristic of species of *Sclerotinia*, are borne free on aerial hyphae and only rarely have remnants of the suscept tissue embedded in them. They tend to be globose when formed free of external pressure. They are, however, often elongate, cylindrical, knobbed, fused, or even irregularly flattened or otherwise irregularly shaped, when formed in natural cavities of the suscept (FIGS. 1–5). The medulla, usually white, is sometimes gray and rarely pinkish. It consists of wide, densely interwoven, thick-walled hyphae, with occasional, small interhyphal spaces. The rind is composed of dark-colored

(usually brown or black), relatively thin-walled palisade cells commonly two or more layers in thickness. The dark color of the rind cells is apparently due to impregnated oxidation products of the dead protoplasmic contents. Sclerotia of this type are normally completely covered by the rind but when formed in artificial culture against the glass side of a test tube usually develop no rind over the contact surface until freed and exposed to the air. If a bit of the rind be cut away from a freshly matured sclerotium, a new rind quickly forms under normal conditions of moisture and air.

The HOLLOW SPHAEROID SCLEROTIUM, characteristic of species of *Monilinia,* is formed just beneath the cuticle in the fruit of the suscept and involves the digestion of the fleshy tissues to a considerable depth. A medulla of large, thick-walled hyphae is covered inwardly as well as outwardly by a well-defined black rind. The structure of the sclerotium is essentially that of the tuberoid type. The rotting away of the enclosed tissues leaves a more or less complete hollow sclerotial sphere of leathery or rubbery consistency (FIG. 10) which wrinkles and shrivels on drying, usually more or less tightly enclosing the seed or unrotted core of the fruit.

The MANTELOID-SPHAERULATE SCLEROTIUM, characteristic of species of *Stromatinia,* presents a unique differentiation of the stroma into two strikingly different forms, due to conditions not yet fully understood. The stroma from which the apothecia arise consists of a thin, subcuticular sclerotium manteling the rhizome or other substrate. It is structurally very similar to the tuberoid sclerotium and is accompanied by tiny black sphaerules of like structure which we have designated *sclerotules.* The latter are borne free on the mycelium and are incapable of giving rise to apothecia. Either form may be produced separately in nature. They may occur together, at least on artificial media.

The DISCOID SCLEROTIA, characteristic of species of *Ciborinia,* are usually found in the necrotized tissue of the leaf of the suscept. They are formed by digesting the tissues between the lower and upper cuticle of the leaf and replacing them with densely interwoven hyphae. These sclerotia are black, usually circular, elongate or ovate-elliptical, thin, of rather uniform thickness, flat or, on drying, somewhat concavo-convex, either persistent in the dead

leaf or dehiscent (FIGS. 6–7). Their structure is essentially that of the tuberoid sclerotia except that the medullary hyphae are more slender and have only moderately thickened walls. Remnants of indigestible vascular elements are usually to be found embedded in the medulla.

The MUMMIOID SCLEROTIA, characteristic of species of *Ciboria*, simulate the form of the stromatized organs (catkin or seed) of the affected plant (FIGS. 11–15). They are dark brown or black. Their structure is essentially that of the discoid sclerotia. They too are formed by the digestion of the suscept tissues and replacement of these with a medullary prosenchyma enclosed in a rind of fungal cells. The medullary hyphae are slender with only moderately thickened walls. Remnants of indigestible vascular elements are usually to be found embedded in the medulla. The stromata of this type usually present little of the external aspect of true sclerotia. They appear to be merely dead overwintered catkins or seeds. It is only on microscopic examination that their true sclerotial nature is seen.

The PLANO-CONVEXOID SCLEROTIA, characteristic of species of *Botryotinia* and *Streptotinia*, are usually formed on or just beneath the cuticle of the necrotized suscept and are in most cases firmly attached. They are black, flat or concave on the attachment surface and more or less erumpent, varying from hemispherical or loaf-shaped to slightly convex (FIGS. 16–24). The rind is wanting or poorly developed over the surface of attachment. The structure of the medulla is fundamentally different from that of the tuberoid type. The hyphae are relatively more slender, thinner-walled, rather loosely interwoven and embedded in a hyaline, flexible matrix. There are no interhyphal spaces. The rind is black and structurally not unlike that of the tuberoid sclerotia.

The SUBSTRATAL STROMATA are all essentially of one type in external form and internal structure. They are characteristic of species of *Rutstroemia* and *Lambertella* where they are visible on the surface of dead leaves and fruits as black patches or crusts or as irregular areas delimited by an irregular, thin, black line. This line consists of the edge view of the rind passing at right angles through the leaf or petiole, blocking off the peculiarly preserved suscept tissues which are threaded through and through with a

loose weft or network of hyaline, slender, anastomosed, thin-walled hyphae. The rind sometimes extends along the leaf surface over veins and veinlets or even spreads out here and there over the blade. Frequently, however, the cuticle itself appears to function in part as a rind. The rind is usually but one cell thick, of slender, irregular, brown- or black-walled cells, forming in surface view a pattern more or less characteristic of each genus. The process by which the fungus solidifies and preserves the enclosed portion of the substrate deserves special investigation. The enclosed tissues which evidently constitute the stored food for the subsequent development of the apothecia show little evidence of other than toxic necrotization. There is no indication of digestion or food storage in the hyphal walls or luminal protoplasm. These blocked-off portions of leaf blade, petiole, fruit, agar, etc., recall the invasion of woody tissue by certain polyporaceous fungi and their formation of a similar "black line" (Campbell, **1933**, **1934**, **1936**). The stroma in *Seaverinia* also is of the substratal type but is rudimentary or vestigial in character. In the one known species it occurs on the surface of rhizomes (FIGS. 34, 35).

In general the spermatia of the Sclerotiniaceae appear at about the time that the stroma develops. The SPERMIDIA (new term proposed to designate all types of spermatial fructification) are of three kinds, *spermodermia* (my coinage), *spermodochia*, and *spermogonia*. A SPERMODERMIUM consists of a palisade or hymenium of spermatiophores of indeterminate extent formed beneath the cuticle along and over the veins and veinlets in the necrotic areas of leaves, as in certain species of *Ciborinia* (FIG. 6), or over the surface of the developing sclerotium, as in species of *Ciboria*. The SPERMODOCHIUM is a fasciculate or tuberculate aggregation of branched spermatiophores arising usually from a single hyphal cell and borne free on the aerial mycelium. Spermodochia rarely exceed a millimeter in diameter individually but are often united into larger masses. They are usually hyaline, white or olivaceous. In certain species, as for example in *Sclerotinia Camelliae* Hansen & Thomas (**1940**), they are black. Spermatiophores may arise singly here and there on the hyphae but they are usually clustered and branched. Spermodochia in some species are produced in specialized lysigenous cavities in the substrate. The re-

sultant structure has been named by us the SPERMODOCHIDIUM (Whetzel **1943**). It does not have a distinct hyphal wall. The SPERMOGONIUM is a pycnidium-like fruit body, usually a millimeter or less in diameter, black, hemispherical or flask-shaped, formed on the surface of the stroma or adjacent to it. It consists of a distinct hyphal-walled conceptacle, the inner surface of the wall giving rise to densely packed, slender, obclavate spermatiophores. The wall is finally ruptured by increasing internal pressure of the mucilaginous mass of spermatia. In all types of spermidia the SPERMATIA are produced semi-endogenously at the tips of the spermatiophores, and tend to form chains which are strikingly evident in certain species. In *Septotinia podophyllina* Whetzel intercalary collar-like bands alternate with the spermatia in the chain, the whole enveloped in a hyaline mucilaginous sheath. When placed in water, separation of the spermatia occurs in such a manner that each carries away one of the collar-like structures as a tiny appendage at its proximal end. This intercalary structure is apparently not present in all species. The spermatia (microconidia) of the Sclerotiniaceae are globose or ovate, 1–4 μ in diameter, thin-walled, hyaline or in mass olivaceous, and each contains near its center a large, well-defined body possibly nuclear in nature (Heuberger **1934**). The spermatia are produced in immense numbers. There can no longer be any doubt that they function as male cells in the process of fertilization. The occasionally reported reproduction of certain species of the Sclerotiniaceae through the germination of these "microconidia" has never been verified by other workers.

The CONIDIDIUM (new term proposed to designate all types of conidial fructification), where present in the life history of species of the Sclerotiniaceae, is one of several types. It is wanting, or at least unknown, in nine of the fifteen genera comprising the family. It is a sporodochium in species of *Monilinia* (FIG. 8) and *Septotinia,* but may consist of scattered or clustered, erect or decumbent, simple or branched conidiophores, bearing the conidia in characteristic manner, as in *Botryotinia* (FIGS. 16, 19), *Streptotinia* (FIG. 22), *Seaverinia* (FIGS. 34, 36), and *Ovulinia.*

The APOTHECIUM is stipitate in all known species of the Sclerotiniaceae. The terminal, expanded, hymenium-bearing portion is

here called the receptacle and is typically cupulate except in one genus where its *Verpa*-like form has caused us to designate it verpoid (FIGS. 25–29). In some of the cupulate species the receptacle remains cup-shaped or funnel-form to complete maturity. In others the cup flattens out to shallow saucer-shaped or disciform, and in a few species becomes typically and pronouncedly reflexed (*e.g. Coprotinia minutula* Whetzel, 1944). In general, species differ from each other very little in the shape of the receptacle. The cups of one species may differ greatly in size, however, from those of another, and there may be considerable variation in size within the limits of a single species. In the group as a whole the cup is characteristically small, even tiny in some forms where it may measure as little as one millimeter in diameter. This is especially true in the genera *Rutstroemia, Ciboria, Botryotinia,* and *Septotinia.* At the other extreme, as in *Sclerotinia Caricis-ampullaceae,* it may reach a diameter of as much as forty millimeters. The outer surface of the receptacle is usually smooth but may be slightly hairy or pruinose. With few exceptions the apothecium is remarkably uniform in color throughout the whole group, being usually brown, commonly some shade of vinaceous brown (Ridgway). A few species have more brightly colored apothecia, especially in the genus *Rutstroemia* where yellow or red shades occur. More rarely the apothecium is white or creamy white. The shade of color in most species varies with the amount of moisture or humidity present. Dried apothecia usually revive readily in water, regaining their natural form and approximately normal color. The color of the hymenial disc is usually of a different shade than that of the outer surface of the receptacle. In the dark-spored species of *Lambertella* and *Martinia* the color of the disc changes instantly on ascospore discharge from dark brown to nearly white. The ASCI are long clavate, the length being in general proportionate to the size of the cup. The ascus tip is thickened, and the pore-plug is usually J +, *i.e.* stains blue with iodine. The ASCOSPORES of all known species may be designated roughly as ellipsoidal, though in a few cases they perhaps more nearly approximate ovoidal or even fusiform. In many species they are somewhat inequilateral, ranging from slightly flattened or concave on one face to almost reniform. Though usually

smooth they may be adorned in various ways. They are commonly hyaline and unicellular, but in *Martinia* and *Lambertella* are brownish or olivaceous, and in some species of *Rutstroemia* are frequently 2–6-septate at late maturity. Septation occurs occasionally also in species of other genera. PARAPHYSES appear to be a structural feature of the hymenium in practically all members of the family. They are typically branched, but often so near the base as to appear simple. The branches, usually three in number, are slender, hyaline, septate, and in some species slightly thickened above. The STIPE is usually more or less concolorous with the receptacle, at least in the upper portion. It tapers toward the base and may be anchored to the substratum by tufts of rhizoidal hyphae. It is commonly smooth or pruinose. The length of the stipe varies considerably, depending on how deeply the stroma is buried. Certain species (*e.g. Coprotinia minutula* Whetzel, **1944**) seem to be naturally long-stalked.

LIFE HISTORY

Most of the Sclerotiniaceae are typically vernal in their fruiting habits. The species of *Rutstroemia* are outstandingly exceptional in developing their apothecia in late summer or autumn. Even the dark-spored species of *Lambertella,* closely related to them, all appear to be spring "bloomers."

Though the members of the family are for the most part pathogenic to the plant tissues in which they live, in general they attack only mature or declining organs such as leaves, stems, and fruits. A few species appear to be saprogens, feeding only on non-living plant substrata. As a group they may be called necrogenic saprophytes. Species in certain of the genera exhibit markedly parasitic tendencies, for example *Ciborinia bifrons* or the gynicolous species of *Ciboria.* These semiparasitic forms usually fail to grow on potato-dextrose agar or other artificial media. Though during the early stages of invasion they exhibit parasitism, taking their nutrients from the living cells, eventually they kill the tissues, effect the major part of their growth, and develop their stromata from the food supply thus made abundantly available to them. At just what point in their development spermatization takes place is known in but few cases and the female mechanism is not yet fully

understood. Homothallism appears to prevail in most if not all species of some of the genera (*Sclerotinia* and *Lambertella*) while in others (*Botryotinia* and *Stromatinia*) heterothallism seems to be the rule. The situation has been studied as yet in too few forms, however, to warrant such generalizations.

The occurrence or nonoccurrence of a conidial stage in the life history provides a basis useful in generic segregation. I have not as yet discovered a case in which this feature fails to be correlated with the type of the stroma. The conidial stage develops during or shortly after the first flush of vegetative growth, generally preceding the formation of spermatia and stromata. In certain species of *Botryotinia* and *Streptotinia* the conidiophores develop also on the overwintered sclerotia and on the vegetative mycelium of the previous season. In several species of *Botryotinia* I have often found individual sclerotia bearing apothecia and tufts of conidiophores at the same time. Such species are thus provided with two kinds of primary inoculum at the opening of the growing season.

In most if not all species successful invasion by the germtube of the conidium or ascospore appears to depend on the presence of certain nutrients or growth-promoting substances in the infection court. This was early pointed out by DeBary in the case of *Sclerotinia sclerotiorum*. These substances appear to be provided by wound extrusions, excretions of the subcuticular tissues, or glandular excretions such as those of stigmatic cells. The spores apparently do not contain sufficient stored nutrients to provide the energy necessary to affect initial access to the food materials of the suscept tissues.

The species of the Sclerotiniaceae appear to be almost entirely confined to the temperate regions of the world. They are especially abundant in the cooler reaches of the north temperate zone. Certain forms like *Martinia panamaensis, Lambertella Jasmini,* and *L. tropicalis* seem to be restricted to a tropical habitat, but as they are known from only a very limited number of collections this conclusion is open to question. Little search for species of the family has been made in the tropics. However, it may be emphasized that the cosmopolitan and omnivorous species *Sclerotinia sclerotiorum* has rarely been found in tropical or subtropical regions ex-

cept in high mountains or in the cooler season. Though there are not many records of the collection of species of this family in the southern hemisphere this is probably due to the fact that few mycologists, especially those interested in the Discomycetes, have collected there.

Some species of *Sclerotinia, e.g. S. sclerotiorum,* under favorable moisture conditions, invade and destroy almost any organ of their suscept. Most members of the genus, however, show a rather definite restriction to certain parts of the plant. The cypericolous and juncicolous species occur largely in the culms. Species of *Monilinia* are largely restricted to fruits, though many of them may also attack flowers, young shoots, and twigs. Species of *Ciborinia* occur almost exclusively in leaves. Though species of *Stromatinia* are pathogens of undergound stems, corms, and roots they occasionally cause lesions on foliage or aboveground stems. *Ciboria* species are definitely amenticolous, some of the species invading catkins only and others ovaries only. The members of most of the other genera, though less specific as to the plant organs attacked, are largely restricted to aboveground parts.

Most members of the family are subjected in nature to periods of drought or winter cold. They maintain themselves in a dormant or inactive condition more by means of the stroma than through possession of long-lived spores. Though under very favorable conditions of uniform dryness and temperature, the conidia, and in some cases the ascospores, remain viable for considerable periods of time, it is doubtful that they do so to any appreciable extent under the variable moisture and temperature conditions that obtain in nature.

Members of the Sclerotiniaceae live and thrive in almost all sorts of habitat, except possibly extreme desert conditions. The low temperatures of the arctic regions do not inhibit the development of some of the sedge-inhabiting species. Many forms are largely restricted to a semi-aquatic habitat, and several show interesting adaptations to it, *e.g.* the sclerotia of *Sclerotinia Duriaeana, S. sulcata,* and *S. scirpicola,* when freed by the bending or breaking over of the enclosing culm (FIG. 3), float on the water of swamp or stream and lodge on mossy hummocks or muddy banks where they fruit the following spring. The sclerotia of the *Carex-*

inhabiting species, *S. longisclerotialis,* remain enclosed in the culms when they fall over and settle to the bottom of swamp pools. Then in the spring the long-stiped apothecia push up through the water to open their tiny cups just above its surface (FIG. 5). The large sclerotia of *S. Caricis-ampullaceae* and *S. Vahliana* remain in the erect dead culms of their suscepts and send up their apothecia through the submerging waters of the swamp. Certain species of *Ciboria* develop their apothecia most abundantly on mossy hummocks or among fallen leaves in or about the margins of shallow pools where the stromata often lie immersed in the water. Many species of *Sclerotinia* and *Monilinia,* however, develop apothecia only from sclerotia buried in the soil or under ground litter or at most in water soaked moss beds. Other forms, especially species of *Rutstroemia,* appear to require little moisture for their development. In general the apothecia of species of the family are found on the ground in moist woodlands or wet swamps.

KEY TO GENERA

I. Stroma a sclerotium, of more or less definite and characteristic form.
  A. Medulla composed of densely interwoven hyphae with occasional small interhyphal spaces; hyphae not embedded in a gelatinous matrix.
    1. Stroma not of the hollow-sphaeroid type; a conidial stage wanting.
      a. Stroma not formed in the tissues of the suscept, and digesting and replacing them; consequently remnants of suscept tissues not commonly embedded in the sclerotium.
        (1) Apothecia arising from a tuberoid sclerotium which, though formed free on aerial mycelium, is sometimes enclosed in natural cavities of the suscept such as the hollow stems of perennials or the culm of sedges ......1. *Sclerotinia,* p. 664
        (2) Apothecia arising from a thin, effuse, subcuticular sclerotium covering (*i.e.* manteling) the affected portion of the suscept; small, black, globose sclerotules also formed on the aerial mycelium ....4. *Stromatinia,* p. 674
      b. Stroma formed in the tissues of the suscept, digesting the available elements and replacing them with a densely interwoven medullary prosenchyma; remnants of resistant suscept tissues commonly remaining embedded among the hyphae of the medulla.
        (1) Stroma an evident, black sclerotium of the discoid type, foliicolous.
          (*a*) Apothecium cupulate to saucer-shaped
          2. *Ciborinia,* p. 667
          (*b*) Apothecium verpoid ....9. *Verpatinia,* p. 690

(2) Stroma a sclerotium of the mummioid type, andricolous or gynicolous, simulating the shape of the stromatized organ of the suscept, usually presenting externally little of the aspect of a sclerotium ....5. *Ciboria*, p. 674

2. Stroma of the hollow-sphaeroid type; a conidial stage present; conidia borne in monilioid chains in sporodochia
3. *Monilinia*, p. 668

B. Medulla lacking interhyphal spaces; medullary hyphae embedded in a hyaline, flexible to gelatinous matrix.

1. Stroma a typical, plano-convexoid sclerotium, loaf-shaped to hemispherical, formed usually on or just beneath the cuticle or epidermis of the suscept and firmly attached to it, flat to concave on the attachment surface, with the rind poorly developed or wanting there.

a. Conidial stage present; ascospores hyaline.

(1) Conidiophore of the *Botrytis cinerea* type; branches not twisted ....6. *Botryotinia*, p. 678

(2) Conidiophore similar; the branches twisted strikingly and characteristically ....8. *Streptotinia*, p. 684

b. Conidial stage wanting; ascospores olive-brown
12. *Martinia*, p. 697

2. Stroma not a typical plano-convexoid sclerotium.

a. Stroma a definite, small, thin, circular to somewhat elongate or angular sclerotium, formed in the tissues of the suscept and digesting them more or less completely; a conidial stage present.

(1) Conidia typically one- or more-septate at maturity, elongate, apically attenuate, basally truncate ....7. *Septotinia*, p. 683

(2) Conidia large, obovoid, unicellular, with a small, basal disjunctor cell ....10. *Ovulinia*, p. 696

b. Stroma not yet observed in nature, in culture of indefinite form and extent; conidial stage wanting; species coprophilous
11. *Coprotinia*, p. 697

II. Stroma indeterminate, of the substratal type, not a definite sclerotium; medulla consisting of a stromatized portion of the substrate permeated with a loose network of narrow, branching, anastomosing, thin-walled hyphae; a thin, black rind of fungus cells delimiting the medulla at least over a portion of its surface.

A. Stromatized portion of the substrate completely blocked off by or surrounded by the rind; conidial stage wanting; ascospores brown, non-septate; spermatia globose or nearly so; spermatiophores not produced on the ascospore ....14. *Lambertella*, p. 701

B. Stromatized portion of the substrate usually less definitely delimited, sometimes rudimentary or wanting; ascospores hyaline.

1. Conidial stage wanting; spermatia broadly ellipsoidal to subglobose; spermatiophores often formed on the mature ascospore; apothecia characteristically produced in late summer or autumn, structurally complex; ascospores sometimes septate at maturity
13. *Rutstroemia*, p. 698

2. Conidial stage present; conidiophore resembling that in *Botryotinia;* conidia minutely tuberculate; apothecia produced in the spring; ascospores non-septate .... 15. *Seaverinia*, p. 703

GENERIC DIAGNOSES

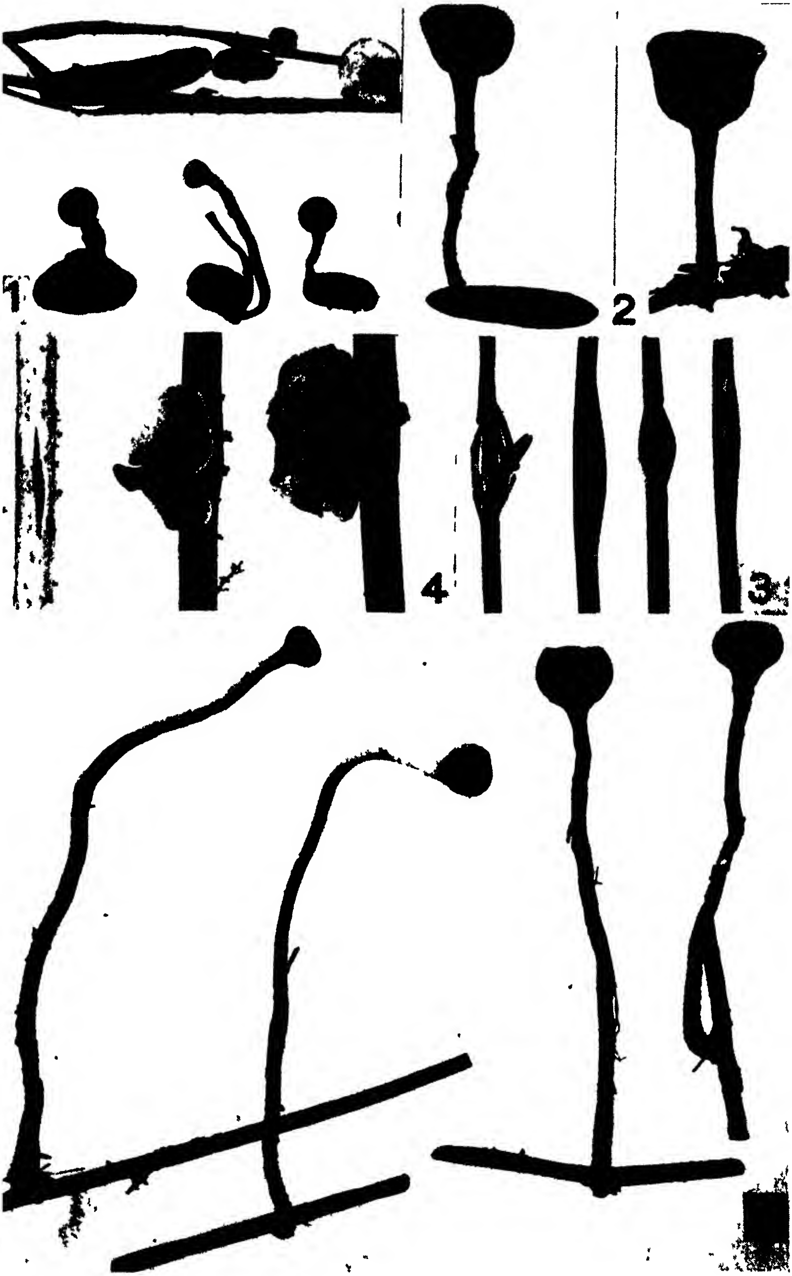
1. SCLEROTINIA Fuckel, Symb. Myc. p. 330. 1870. **(Type genus)**

(FIGS. 1–5)

Stroma a definite sclerotium of the tuberoid type, formed free on aerial hyphae and in consequence loosely attached to the substratum and tending to be globose, at most loosely enclosed in natural cavities of the suscept such as the hollow stems of perennials (FIG. 1) or the culms of sedges (FIGS. 2–5), and then often elongate, cylindrical, knobbed or even flattened or otherwise irregularly shaped; *medulla* usually white, composed of densely interwoven, broad, thick-walled, hyphal prosenchyma with occasional small interhyphal spaces; a gelatinous matrix lacking; *rind* enveloping the sclerotium completely, usually composed of two or more layers of dark-colored, thin-walled, palisade cells; *appressoria* commonly formed in culture but less profusely than in *Botryotinia; spermidium* a spermodochium, borne free and naked, or enclosed in spermodochidia, *i.e.* in specialized lysigenous cavities in the suscept tissues (Whetzel **1943**); *spermatia* globose to slightly ovate, hyaline or in mass olivaceous; *conididium* wanting; *apothecia* cupulate to funnel-form, at maturity shallow saucer-shaped to flat-expanded, some shade of brown, commonly vinaceous brown (Ridgway), 2 to 40 mm. in diameter; *ascospores* 1-celled, hyaline, ellipsoidal, inequilateral, rarely reniform.

Type species: *Sclerotinia sclerotiorum* (Lib.) DeBary, Vergl. Morph. Biol. der Pilze, Mycet. Bact. 1884.—*Syn. Peziza sclero-*

FIGS. 1–5. *Sclerotinia.* 1, *S. sclerotiorum,* type species of the type genus of the family, on *Ranunculus septentrionalis,* apothecia arising from sclerotia formed in overwintered stems, × 2 (*C15622*). 2, 3, *S. sulcata* on *Carex stricta.* 2, two three-sided sclerotia, formed in hollow culms, each bearing an apothecium, × 2 (*C11515*). 3, sclerotia in process of bursting from the culm, Nat. size (*C14747*). 4, *S. Curreyana* on *Juncus effusus,* sclerotia germinating *in situ* in hollow culms and bearing apothecia, Nat. size (*C20198*). 5, *S. longisclerotialis* on *Carex prairea,* unusually long, cylindrical sclerotia bearing apothecia, × 2 (*C11516*).



FIGS. 1–5.

tiorum Lib., Exs. No. *326, Sclerotinia Libertiana* Fuckel, Symb. Myc. p. 331. 1870.

Included species:

S. Caricis-ampullaceae Nyberg, Mem. Soc. Fauna Fl. Fenn. **10**: 20–23. 1894; see Whetzel, Mycologia **35**: 385. 1943, also Farlowia **2**: No. 3. Jan. 1946 (in press).

S. Curreyana (Berkeley) Karsten, Revisio Monogr. p. 123. 1885.—*Syn. Peziza Curreyana* Berk., *in* Currey, Jour. Linn. Soc. **1**: 147. 1857; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press), also Mycologia **36**: 426. 1944.

S. Duriaeana (Tul.) Rehm, Hedwigia **21**: 66. 1882.—*Syn. Peziza Duriaeana* Tulasne, Fung. Carp. **1**: 103. 1861, and **3**: 203. 1865; see Whetzel, Mycologia **21**: 19. 1929, and **36**: 426. 1944, also Farlowia **2**: No. 3. Jan. 1946 (in press).

S. intermedia Ramsey, Phytopathology **14**: 324. 1924.

S. longisclerotialis Whetzel, Mycologia **21**: 24. 1929; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press).

S. minor Jagger, Jour. Agric. Res. **20**: 333. 1920.

S. Panacis Rankin, Phytopathology **2**: 30. 1912.

S. sativa Drayton & Groves, Mycologia **35**: 526. 1943.

S. scirpicola Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3, 822. 1893; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press).

S. sulcata Whetzel, Mycologia **21**: 15. 1929.—*Syn. Sclerotium sulcatum* Roberge, in herb. Desmazières, Ann. Sci. Nat. III. **16**: 329. 1851; see Whetzel, Farlowia **2**: No. 3. Jan. 1946 (in press).

S. Trifoliorum Eriksson, Kongl. Landtbr. Akad. Handl. og. No. 1. p. 28–42. 1880.—*Syn. Peziza ciborioides* Hoffm., Icon. Anal. Fung. III. p. 65. 1863.

S. Vahliana Rostr., *in* Tillaeg til "Grönland Svampe (1888)." Saertryk of Meddel. om Grönland **3**: 607–608. 1891.

Two new species of *Sclerotinia* are described and a transfer to *Sclerotinia* from *Ciboria* is made in my paper (Whetzel **1946**) on cypericolous and juncicolous species.

2. **Ciborinia** Whetzel, gen. nov.[3]

(FIGS. 6, 7)

Stroma a definite sclerotium of the discoid type with black rind and white medulla, usually circular or ovate-elliptical to elongate in outline, thin, black, flat or on drying somewhat concavo-convex, foliicolous, usually erumpent and persistent, sometimes deciduous, digesting the less resistant tissues and replacing them with densely interwoven hyphae among which remnants of the resistant vascular elements of the leaf commonly remain embedded, essentially the same structurally as the tuberoid sclerotium except that the hyphae of the medulla are more slender and thinner-walled; *spermidium* a spermodermium, subcuticular along the leaf veins (FIG. 6); *spermátia* globose or ovate, hyaline, in mass pale yellowish; *conididium* wanting; *apothecia* stipitate, one to several arising from the sclerotium, cupulate to shallow saucer-shaped or flat-expanded, small to medium, 1–5 mm. in diameter, cinnamon brown to avellaneous (Ridgway), sometimes paler, rarely reddish (FIG. 7); *ascus* usually 8-spored; *ascospores* unicellular, hyaline, ellipsoidal or ovoid, usually slightly inequilateral; *paraphyses* slender, sometimes swollen at the tip.

Apothecium ex sclerotio definito oriundum, cupulatum vel subpatelliforme, parvum vel medium, cinnamomeo-fuscum vel avellaneum (Ridgway), interdum pallidius, raro rufum; sclerotium orbiculatum ovato-ellipticumve, vel

[3] Professor Whetzel had made considerable progress in the study of the species of this genus. In an unfinished manuscript he states that twelve species studied by him belong here. Eight of these form their sclerotia in the leaves of deciduous trees—poplars, willows, and maples. Four occur in the leaves of *Trillium, Erythronium,* and *Viola.* The apothecia of all are to be found in late spring or early summer arising from sclerotia on or about the debris of their various substrata. The as yet unpublished species bear tentative names in the herbarium at Cornell University, and the material is accompanied by photographs and notes. Some members of the genus make little or no growth on the usual sorts of culture media. Others develop readily on potato dextrose agar, where they form characteristically thin, ovate to circular, crust-like sclerotia. The mycelium in culture resembles that of *Sclerotinia* in being hyaline or in having only occasional brown hyphae, in contrast to that of *Ciboria* where the hyphae turn brown early. The apothecia in form, size, structure, color, and spore characters are indistinguishable from those of *Ciboria,* and in general are smaller than those of *Sclerotinia.* In sclerotial characters *Ciborinia* is intermediate between these genera. In lacking a conidial stage it agrees with both of them.

elongatum, tenue, nigrum, discoideum, quando siccum concavo-convexum, in folii tissibus formatum, pro illis hyphas dense intertextas substituens, indigestis resistentiorum elementorum reliquiis manentibus, plerumque erumpidum perstatumque, interdum deciduum, in structura simile sclerotii *Sclerotiniae;* medulla alba, aliquando cum intervallis interhyphas; matrix gelatinosa deficiens; spermatia in spermodermiis subcuticulariis formata; status conideus deficiens; ascosporae hyalinae, ellipsoideae vel ovatae, unicellulares, inaequilaterales.

Type species: Ciborinia bifrons (Whetzel) comb. nov.—*Syn. Sclerotium bifrons* Ellis & Ev., *in* Sacc. Syll. Fung. **14**: 1169. 1899 (*Sclerotium bifrons* Ellis & Ev., *nom. nud.* N. Am. Fungi No. 2554), *Sclerotinia bifrons* Whetzel, Mycologia **32**: 126. 1940 (not *Sclerotinia bifrons* Seaver & Shope, Mycologia **22**: 1–8. 1930), *Sclerotinia Whetzelii* Seaver, Mycologia **32**: 127. 1940; see Pomerleau, Canadian Journal of Research **18**: 199–214. 1940.

Included species:

- C. **Candolleana** (Lév.) comb. nov.—*Syn. Peziza Candolleana* Lév., Ann. Sci. Nat. II. **20**: 233. 1843, *Sclerotinia Candolleana* (Lév.) Fuckel, Symb. Myc. p. 330. 1870.
- C. **confundens** (Whetzel) comb. nov.—*Syn. Sclerotinia confundens* Whetzel, Mycologia **32**: 126. 1940, *S. bifrons* Seaver & Shope, Mycologia **22**: 1–8. 1930.
- C. **Erythronii** (Whetzel) comb. nov.—*Syn. Sclerotinia Erythronii* Whetzel, Mycologia **18**: 232. *pl. 27–29. fig. 1.* 1926.
- C. **foliicola** (Cash & Davidson) comb. nov.—*Syn. Sclerotinia foliicola* Cash & Davidson, Mycologia **25**: 269. 1933.
- C. **gracilis** (Clements) comb. nov.—*Syn. Sclerotinia gracilis* Clements, Contrib. Bot. Dept. Univ. Nebr. n. s. **3**: 47. 1892.

3. MONILINIA Honey, Mycologia **20**: 153. 1928.

(FIGS. 8–10)

Stroma a definite sclerotium of the hollow-sphaeroid type, fructicolous, formed just beneath the cuticle, digesting the fleshy tissues

FIGS. 6, 7. *Ciborinia bifrons,* type species, on *Populus tremuloides.* 6, typical discoid sclerotia with subcuticular spermodermia along the midrib and veins, × 2 (*C14755*). 7, apothecia arising from sclerotia. Nat. size (*C11803*).

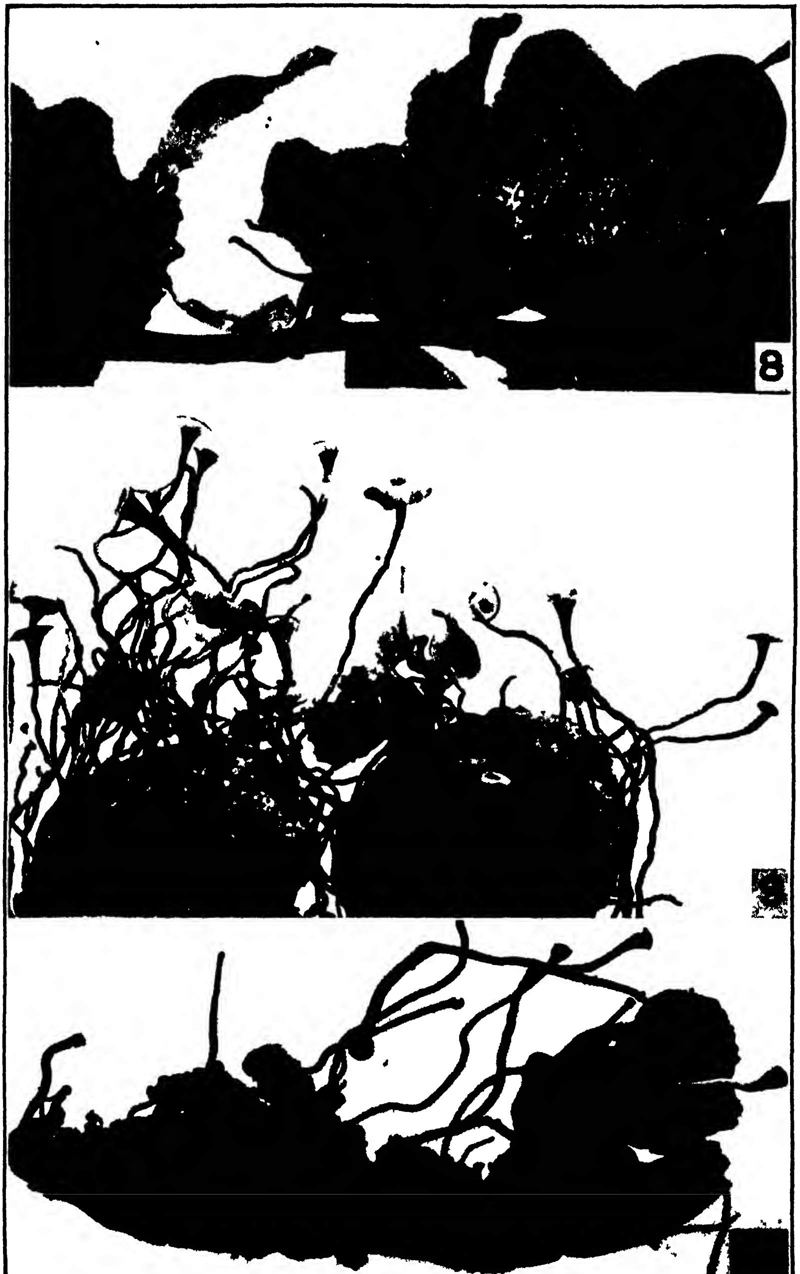
Figs. 6, 7.

of the fruit to a considerable depth, and replacing them with a layer of broad, thick-walled, densely interwoven hyphae forming a more or less complete hollow sphere usually enclosing the core or seed (FIG. 10); this peripheral prosenchymatous layer, consisting chiefly of the medulla of the sclerotium, covered on both its inner and outer surfaces with a thin black rind; *mature sclerotium* of leathery or rubbery consistency, on drying becoming wrinkled and hard; *medulla* structurally like that of the tuberoid sclerotium; *spermidium* unknown in nature, formed as a spermodochium in culture media; *spermatia* globose or slightly ovate, hyaline; *conidium* a sporodochium (FIG. 8); *conidia* unicellular, ellipsoidal or lemon-shaped, formed in monilioid chains, hyaline, in mass grayish or buff, with or without disjunctors between adjacent conidia; *apothecia* funnel-form or cupulate, rarely flat-expanded (FIG. 9), some shade of brown, usually vinaceous brown (Ridgway); *asci* 8-spored, rarely 4-spored; *ascospores* unicellular, ellipsoidal, often slightly flattened on one side, hyaline.[4]

Type species: *Monilinia fructicola* (Winter) Honey, Mycologia **20**: 153. 1928.—*Syn. Ciboria fructicola* Winter, Hedwigia **22**: 131. 1883, *Sclerotinia fructicola* (Winter) Rehm, *in* Sacc. Syll. Fung. **18**: 41. 1906.

[4] Professor Whetzel mailed a copy of the portion of his manuscript dealing with *Monilinia* to Dr. E. E. Honey as soon as the first draft of it was finished. He asked him to make corrections and suggestions, and solicited his aid in checking and completing the citations given in the appended tentative list of included species. Unfortunately, Dr. Honey's reply arrived after Professor Whetzel had become too ill to give it consideration. Concerning the structure of the stroma, Dr. Honey made comments in his letter which we feel may be appropriately incorporated here. Whetzel believed Honey's conception of the stroma in *Monilinia* as a "pseudosclerotium" to be erroneous and asserted that the description and illustrations published by Honey (**1928**) "were made from immature stromata." Honey replied that his studies were based on overwintered stromata bearing apothecial fundaments. Also he said that in some species of the genus the stroma, while admittedly hollow-sphaeroid, is definitely clathrate, and in some others is actually not hollow. The following citations were given detailed consideration by Dr. Honey, and corrections made by him have been incorporated.

FIGS. 8–10. *Monilinia fructicola.* 8, sporodochia on fruit of *Prunus domestica* (cultivated blue plum), Nat. size (*C24976*). 9, overwintered fruit of *Prunus Persica* (cultivated peach) bearing apothecia, reduced (*C12602*). 10, one such fruit torn open to demonstrate the hollow-sphaeroid character of the sclerotium.



FIGS. 8–10.

Included species:

M. Amelanchieris (Reade) Honey, Mycologia **34**: 575. 1942. —*Syn. Sclerotinia Amelanchieris* Reade (based on conidial stage), Ann. Myc. **6**: 114. 1908.

M. Ariae (Schell.) comb. nov.—*Syn. Sclerotinia Ariae* Schell., Centralbl. Bakt. II. Abt. **12**: 735. 1904.

M. Aucupariae (Ludwig) comb. nov.—*Syn. Sclerotinia Aucupariae* Ludwig, *in* Woronin. Mem. Acad. Sci. St. Petersbourg VIII. **2**: No. 1. 15–20. 1895.

M. Azaleae Honey, Phytopathology **30**: 537–539. 1940.

M. baccarum (Schröt.) comb. nov.—*Syn. Rutstroemia (Sclerotinia) baccarum* Schrot., Hedwigia **18**: 180. 1879, *Sclerotinia baccarum* (Schrot.) Rehm, Hedwigia **24**: 9. 1885.

M. Corni (Reade) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Corni* Reade (based on conidial stage), Ann. Myc. **6**: 113. 1908.

M. Cydoniae (Schell.) comb. nov.—*Syn. Sclerotinia Cydoniae* Schellenberg, Centralbl. Bakt. II. Abt. **17**: 189. 1907; *see* Wormald, Trans. Brit. Myc. Soc. **10**: 303–306. *pl. 18.* 1926.

M. demissa (Dana) Honey, Amer. Jour. Bot. **23**: 106. 1936.—*Syn. Sclerotinia demissa* Dana, Phytopathology **11**: 228. 1921.

M. fructigena (Aderh. & Ruhl.) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia fructigena* Aderh. & Ruhl., Arb. Biol. Abt. Land.-Forstw. K. Gesundheits **4**: 430. 1905.

M. Johnsonii (Ellis & Ev.) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Ciboria Johnsonii* Ellis & Everhart, Proc. Phil. Acad. Nat. Sci. **46**: 348. 1895, *Sclerotinia Crataegi* Magnus, Ber. Deutsch. Bot. Gesell. **23**: 197–202. 1905, *Sclerotinia Johnsonii* (Ellis & Ev.) Rehm, Ann. Myc. **4**: 338. 1906.

M. laxa (Aderh. & Ruhl.) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Cerasi* Woronin (based on conidial stage), Mem. Acad. Sci. St. Petersbourg VII. **36**: No. 6. 39. 1888, *S. laxa* Aderhold & Ruhland, Arb. Land.- Forstw. K. Gesundheits **4**: 427. 1905, *S. cinerea* (Bonorden) Schröt. (based on conidial stage), Krypt. Fl. Schlesien **3**: 67. 1893,

S. cinerea Wormald, Ann. Bot. **35**: 131. *pl. 6, 7.* 1921, *S. cinerea* f. *Pruni* Wormald, Ann. Bot. **33**: 374. 1919 and **34**: 167. 1920; *see* Harrison, T. H. Jour. and Proc. Royal Soc. N. South Wales **67**: 132–177. 1933.

M. Ledi (Nawaschin) comb. nov.—*Syn. Sclerotinia Ledi* Nawaschin, Ber. Deut. Bot. Gesell. **12**: 117. 1894, *S. heteroica* Woronin & Nawaschin, Ber. Deut. Bot. Gesell. **12**: 187. 1894, also Zeitschrift Pflanzenk. **6**: 129–140. *pl. 3, 4.* 1896.

M. Mali (Takahashi) comb. nov.—*Syn. Sclerotinia Mali* Takahashi, Bot. Mag. Tokyo **29**: 217. 1915.

M. megalospora (Woronin) comb. nov.—*Syn. Sclerotinia megalospora* Woronin, Mem. Acad. Sci. St. Pétersbourg VII. **36**: No. 6. 35–40. 1888.

M. Mespili (Schell.) comb. nov.—*Syn. Sclerotinia Mespili* Schell., Centralbl. Bakt. II. Abt. **17**: 188–196. 1907.

M. Oxycocci (Woronin) Honey, Amer. Jour. Bot. **23**: 105. 1936.—*Syn. Sclerotinia Oxycocci* Woronin, Mem. Acad. Sci. St. Petersbourg VII. **36**: No. 6. 28–30. 1888.

M. Padi (Woronin) Honey, Amer. Jour. Bot. **23**: 105. 1936. —*Syn. Sclerotinia Padi* Woronin, Mem. Acad. Sci. St. Petersbourg VIII. **2**: No. 1. 3–14. 1895, *S. angustior* Reade, Ann. Myc. **6**: 113. 1908.

M. Polycodii (Reade) Honey, Amer. Jour. Bot. **23**: 106. 1936. —*Syn. Sclerotinia Polycodii* Reade, Ann. Myc. **6**: 110. 1908.

M. Rhododendri (Fischer) comb. nov.—*Syn. Sclerotinia Rhododendri* Fischer, Ber. Schw. Bot. Gesells. **4**: 1–18. 1894.

M. Seaveri (Rehm) Honey, Amer. Jour. Bot. **23**: 105. 1936.— *Syn. Sclerotinia Seaveri* Rehm, Ann. Myc. **3**: 519. 1905.

M. Urnula (Wein.) comb. nov.—*Syn. Ciboria Urnula* Weinmann, Hymeno- Gastero-Mycetes p. 459. 1836, *Sclerotinia Vaccinii* Woronin, Mem. Acad. Sci. St. Petersbourg VII. **36**: No. 6. 3–27. 1888, *S. Urnula* (Wein.) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 804. 1893; *see* Woronin, Mem. Acad. Sci. St. Petersbourg VIII. **2**: No. 1. 4. footnote 3. 1895.

M. Vaccinii-corymbosi (Reade) Honey, Amer. Jour. Bot. **23**:

105. 1936.—*Syn. Sclerotinia Vaccinii-corymbosi* Reade, Ann. Myc. **6**: 109. 1908.

4. STROMATINIA Boudier,[5] Hist. Class. Discom. Eu. p. 108. 1907.

Stroma of the type here termed manteloid-sphaerulate, two kinds of sclerotia being formed; apothecia arising from a thin, black, subcuticular, effuse sclerotium covering or manteling the affected portion of the suscept; small, black sphaerules (*sclerotules*) borne free on the mycelium and not giving rise to apothecia; both kinds of sclerotia structurally of the tuberoid type; either sort produced separately; *sclerotules* wanting or unknown in most species under natural conditions but developing abundantly in artificial media; *spermidium* a spermodochium; *spermatia* globose; *conididium* unknown; *apothecia* resembling those of *Sclerotinia; ascospores* hyaline, unicellular.

Type species: *Stromatinia Rapulum* [Bull.] Boudier, Hist. Class. Discom. Eu. p. 108. 1907.—*Syn. Peziza Rapulum* Bull. Champ. Fr. p. 295. *pl. 485. fig. 3.* 1790.

Included species:

S. cepivorum (Berk.) Whetzel, comb. nov.—*Syn. Sclerotium cepivorum* Berk., Ann. Mag. Nat. Hist. **6**: 359. 1841.—The manteling stroma and *apothecia* are *unknown* in this species, but sclerotules are formed both in culture and under natural conditions.

S. Gladioli (Drayton) Whetzel, comb. nov.—*Syn. Sclerotinia Gladioli* (Massey) Drayton, Phytopathology **24**: 400. 1934, *Sclerotium Gladioli* Massey, Phytopathology **18**: 519–529. 1928.

S. Paridis Boudier, Hist. Class. Discom. Eu. p. 108. 1907.

S. Smilacinae Durand, Bull. Torrey Club **29**: 462. 1902.

5. CIBORIA Fuckel, Symb. Myc. p. 311. 1870.

[5] Though Professor Whetzel was attempting to bring together materials for a monographic treatment of this genus, it is clear, from an examination of his notes and correspondence, that his studies were not approaching completion. He was apparently less certain of the generic characters and limits in this case than in any other genus of the family and was in doubt concerning several species not yet adequately investigated.

(FIGS. 11–15)

Stroma a sclerotium of the mummioid type, dark brown or black, andricolous (in male catkins) or gynicolous (in seed), simulating the shape of the stromatized organ of the suscept and usually presenting externally little of the aspect of a sclerotium (FIGS. 11–15), structurally, however, essentially like the discoid sclerotium, formed by digestion of the less resistant elements of the suscept tissues and their replacement with a medullary prosenchyma enclosed in a rind of fungus cells, in culture thin, plate-like, consisting of a dark rind and a white medulla; medullary hyphae slender, with remnants of undigested vascular elements usually embedded among them; *appressoria* unknown; *spermidium* a spermodermium manteling the developing sclerotium; *spermatia* globose or ovate, hyaline or in mass faintly brownish; *conididium* wanting; *apothecia* cupulate to shallow saucer-shaped, often becoming flat-expanded or even strongly reflexed, usually some shade of brown, especially vinaceous brown (Ridgway), sometimes red or yellow, rarely white, small to medium sized, brittle waxy to tough leathery; *asci* 8-spored (rarely 4-spored); *paraphyses* hyaline or colored, filiform, slightly thickened above; *ascospores* ellipsoidal, inequilateral, unicellular, hyaline, smooth or minutely ornamented with elevations or depressions.

Type species: *Ciboria Caucus* (Reb.) Fuckel, Symb. Myc. p. 311. 1870.—*Syn. Peziza Caucus* Rebentisch, Prodr. Fl. Neomarch. p. 386. 1804.

Included species:

C. Acerina Whetzel & Buchwald, Mycologia **28**: 516. 1936.

C. Alni (Maul) comb. nov.—*Syn. Sclerotinia Alni* Maul, Hedwigia **33**: 215. 1894.

C. amentacea (Balbis) Fuckel, Symb. Myc. p. 311. 1870.—*Syn. Peziza amentacea* Balb., Mem. Acad. Turin II. p. 79. *t. 2.* 1805.

C. amenti (Batsch) comb. nov.—*Syn. Peziza amenti* Batsch, Elench. Fung. Cont. **1**: 211–214. 1786, *Helotium amenti* (Batsch) Fuckel, Symb. Myc. p. 313. 1870.

C. Aschersoniana (Henn. & Plött.) comb. nov.—*Syn. Sclerotinia Aschersoniana* Hennings & Plöttner, Verh. Bot. Ver. Prov. Brandenburg **41**: 9. 1900.

C. Betulae (Woronin) White, Lloydia **4**: 171, 238. 1941.—*Syn. Sclerotinia Betulae* Woronin, *in* Nawaschin, *thesis,* St. Petersbourg, 1893.

C. carunculoides (Siegler & Jenkins) Whetzel & F. A. Wolf, Mycologia **37**: 476–491. 1945.—*Syn. Sclerotinia carunculoides* Siegler & Jenkins, Science n. s. **55**: 353. 1923, and Jour. Agric. Res. **23**: 833. 1923.

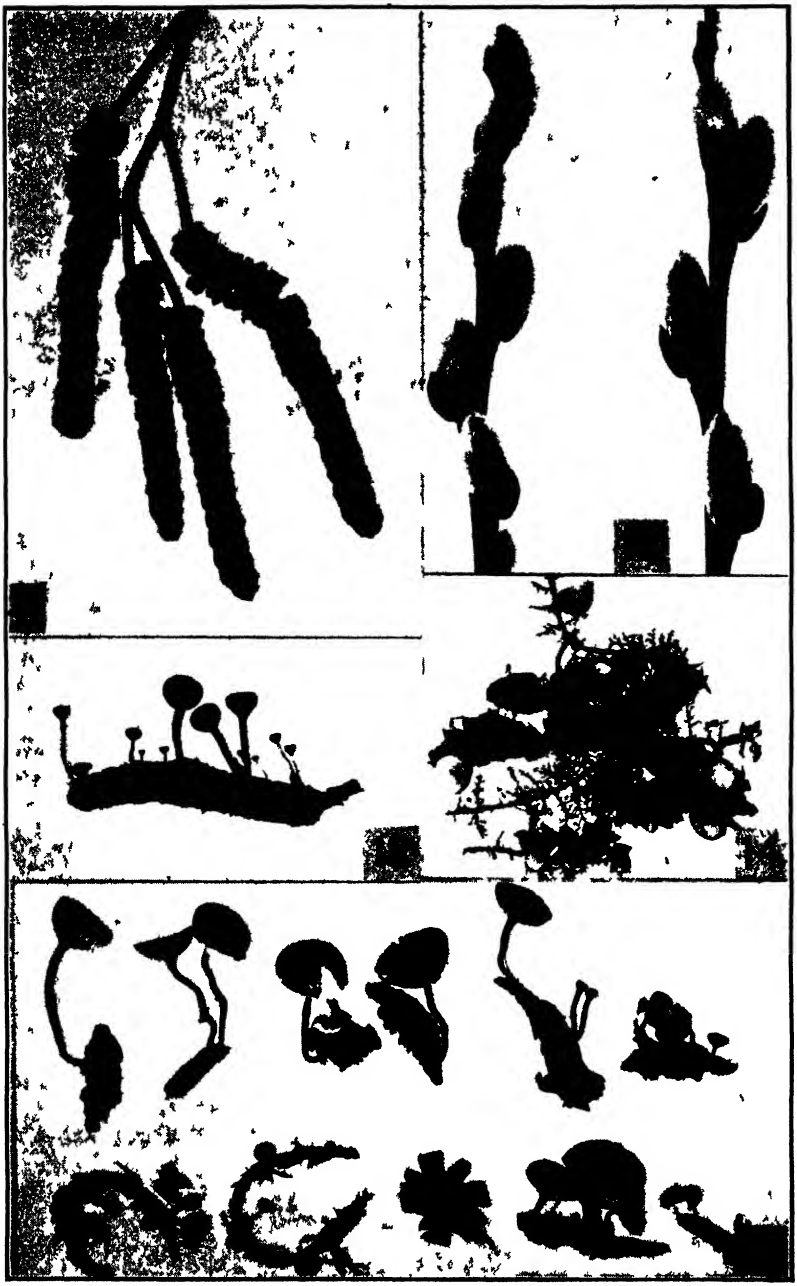
C. Carpini (Batsch) comb. nov.—*Syn. Peziza Carpini* Batsch, Elench. Fung. Cont. **1**: 215–216. 1786.

C. Coryli (Schell.) comb. nov.—*Syn. Sclerotinia Coryli* Schellenberg, Ber. Deut. Bot. Gesell. **24**: 505–511. 1905.

C. Shiraiana (Henn.) Whetzel, Mycologia **37**: 489. 1945.—*Syn. Sclerotinia Shiraiana* Hennings, *in* Engler's Jahrb. **28**: 278. 1900.[6]

[6] STATEMENT BY H. M. FITZPATRICK. The paper up to this point was written by Professor Whetzel. Here, too ill to continue, he put down his pencil. A few weeks later he died. The manuscript was his first draft, and he unquestionably intended to give it critical revision before publication. Consequently, though it is presented here largely in the form in which he prepared it, a considerable number of minor alterations have been necessary, especially in phraseology.—The remainder of the paper, beginning with the genus *Botryotinia,* has been written by me. All the footnotes are mine. Also I prepared the family diagnosis and key to genera and have inserted these above in the portion of the paper written by Whetzel. Though not a student of the taxonomy of the Discomycetes, I was more or less closely associated with him, in the Department of Plant Pathology of Cornell University, throughout all the years in which he was engaged in the study of the Sclerotiniaceae. I understood his viewpoints, terminology, and methods and was familiar with his system of filing notes, cultures, herbarium specimens, photographs, and correspondence. He was a methodical man, and his records were left in available condition. The ten generic diagnoses which follow were based by me on these records, on his statements in the preceding portion of this paper, and on his publications and those of his students. The names applied to the

FIGS. 11–15. *Ciboria.* 11, 12, *C. amentacea* on male catkins of *Alnus incana,* Nat. size (*C23366*). 11, mummification in progress five days after inoculation with shooting ascospores. 12, young apothecia developing from a mummified overwintered male catkin. 13, twigs of *Salix discolor* with normal female catkins, Nat. size. 14, 15, mummified overwintered catkins of *S. discolor* bearing apothecia of *Ciboria Caucus,* type species, Nat. size. 14, female catkins on moss-covered ground beneath the tree (*C24193*). 15, male and female catkins (*C17464*).



FIGS. 11–15

6. **Botryotinia** Whetzel, gen. nov.

(FIGS. 16–20)

Stroma a definite black sclerotium of the type here designated plano-convexoid, characteristically flattened, loaf-shaped or hemispherical, formed usually on or just beneath the cuticle or epidermis of the suscept and firmly attached to it (FIGS. 16, 17), if covered, then in time erumpent, flat to concave on the attachment surface with the rind poorly developed or wanting there, differing thus from the tuberoid sclerotia of *Sclerotinia* which are formed free on aerial hyphae and in consequence are loosely attached to the surface of the substratum or at most are loosely enclosed in cavities of the suscept such as the hollow stems of perennials or the culms of sedges; *medulla* differing fundamentally in structure from that of the sclerotium of *Sclerotinia*, the hyphae being more slender, thinner-walled, more loosely interwoven, and embedded in a hyaline, flexible to gelatinous matrix, there being no interhyphal spaces; this structural difference clearly illustrated by DeBary (**1887**: p. 31. *fig. 13, 14*); *rind* black, distinctly differentiated, more or less definitely pseudoparenchymatous or palisade-like (FIG. 18), essentially like that in *Sclerotinia; spermidium* a spermodochium, bearing globose spermatia on branching spermatiophores, the

five new genera were selected by him. The effort has been made to complete the manuscript as far as possible in the form in which he would have written it. Though aware that he might have embodied material of which his notes give no indication, I am convinced that the paper incorporates the features that he expected to stress. As he had not yet selected illustrations, I have chosen from the files the photographs which seem most suitable. All of these, except the two used for figures 17 and 29, were made by Mr. W. R. Fisher, photographer in the Department of Plant Pathology. Throughout the years his excellent photographs have illustrated Professor Whetzel's papers. The sections of stromata, photographed for figures 28, 31, and 34, were made for my use by Mr. Bert Lear, Fellow in the Department. The Latin diagnoses were prepared, at my request, by Mrs. M. W. Allen, Scientific Assistant in the Department of Botany.—The completed manuscript was submitted for criticism to Dr. F. L. Drayton, Dr. J. Walton Groves, Dr. Edwin E. Honey, and Dr. W. Lawrence White. Most of the changes suggested by them have been made, and the paper as here published has in general their approval. We are united in a feeling of satisfaction that this summarization of Professor Whetzel's years of effort is not lost to science and will stand as a memorial to him.

entire structure enveloped in a mucilaginous matrix and drying to a waxy consistency; *conidiophores* (*Botrytis* of the *cinerea* type) erect, fasciculate, usually more or less olivaceous, often proliferating, bearing dense clusters of conidia on sterigmata on short clustered side branches which are usually hyaline and terminally swollen (FIGS. 16, 19); *conidia* smooth, unicellular, hyaline to light brown, ovate to subglobose or subpyriform, their production usually more profuse in a dry atmosphere than under conditions of high humidity; *apothecia* cupulate and stalked, some shade of brown; cup varying from infundibuliform to discoid, the margin in age sometimes reflexed (FIG. 16); *ascospores* hyaline, unicellular, ellipsoidal; *apothecial characters* essentially as in *Sclerotinia;* mycelial tips in culture on contacting the glass surface tending to branch profusely to form characteristic masses of *appressoria* which are more typical of this genus than of any other; their structure and development well illustrated by Istvánffi (**1905**).

Apothecia vere ut in *Sclerotinia;* apothecium ex sclerotio definito oriundum, stipitatum, cupulatum, fuscum; cupula infundibuliformis vel discoidea, margine interdum reflexa; ascosporae hyalinae, unicellulares, ellipsoideae; sclerotium hemisphaericum vel subhemisphaericum, plerumque ad substratum firme adnatum, haec superficie plana et cortice ibi tenue formato vel deficiente; medulla in structura ab *Sclerotinia* recedit, hyphis gracilioribus, laxius intertextis, cum septis tenuioribus, per matricem gelatinosam circumplexisque, intervallis inter hyphas deficientibus; spermatia in spermodochiis sustenta; conidiophorae ut in *Botryte cinerea;* conidia laevia unicellulares, hyalina vel subfusca, ovata vel subglobosa vel subpyriformia; apices hyphorum prominentes singularesque massas appressorium in cultura formantes.

Type species: Botryotinia convoluta (Drayton) Whetzel, comb. nov.—*Syn. Botrytis convoluta* Whetzel & Drayton, Mycologia **24**: 475. 1932, *Sclerotinia convoluta* Drayton, Mycologia **29**: 314–316. 1937.

Included species:

B. Fuckeliana (DeBary) Whetzel, comb. nov.—*Syn. Botrytis cinerea* Pers., Syn. Fung. p. 690. 1801, *Peziza Fuckeliana* DeBary, Morphol. Phys. Pilze, Flechten, Myxomyceten p. 30. 1866, *Sclerotinia Fuckeliana* (DeBary) Fuckel, Symb. Myc. p. 330. 1869.

B. Porri (Beyma Thoe Kingma) Whetzel, comb. nov.—*Syn. Sclerotinia Porri* Beyma Thoe Kingma, Medel. Phytopath. Lab. Willie Commelin Scholten **10**: 43–46. 1927.

B. Ricini (Godfrey) Whetzel, comb. nov.—*Syn. Sclerotinia Ricini* Godfrey, Phytopathology **9**: 565–567. 1919.

Though many diverse conidial fungi have been placed in the form-genus *Botrytis,* Whetzel had long restricted his use of the name to the species of the so-called *cinerea* type. In addition to botryose conidiophores and conidia, these species are characterized by the possession of spermatia, appressoria, and sclerotia. Some of them have been found to form apothecia, and possibly all do so. Several have been transferred to the genus *Sclerotinia.* Convinced that they all constitute a natural group, and desiring to avoid further confusion with the form-genus *Botrytis,* Whetzel here erects the new genus *Botryotinia* for them.

Persoon described *Botrytis cinerea* from material on cabbage leaves. When Whetzel examined the type specimen it no longer contained conidia or sclerotia. As several species of *Botrytis* are commonly found on stored cabbage in Europe and America, and as Persoon's brief description is applicable to a wide range of material, it is impossible to state with certainty to what form he applied the name *B. cinerea.* It was Whetzel's practice to allude to all such fungi merely as *Botrytis* of the *cinerea* type. He emphasized that the apothecia are of little value in taxonomic separations and stated that specific identities in the group must rest primarily on characters of the conidial and sclerotial stages. The difficulties involved in attempting to define specific limits have been indicated by the results of Groves and Drayton (**1939**) in extensive cultural studies with apothecial material derived from a large number of conidial isolates.

FIGS. 16–20. *Botryotinia.* 16, *Botryotinia* sp. on *Iris versicolor,* apothecia and tufts of condiophores arising from sclerotia on overwintered leaves lying on water and wet soil, × 2 (*C29085*). 17, 18, *Botrytis* sp. on tulip (*15248*). 17, typically loaf-shaped, firmly attached sclerotia on outer bulb scales typical of *Botryotinia,* Nat. size (photo by Louise Dosdall). 18, structure of sclerotium as shown in free hand section, × 300. 19, 20, *Botryotinia convoluta,* type species, on rhizomatous iris (*C19223*). 19, base of conidiophore fascicle showing origin of conidiophores from large, dark, thick-walled, mycelial cells. 20, petri dish culture bearing typically convoluted sclerotia, Nat. size.

FIGS. 16–20.

Early in his studies of sclerotial fungi, Whetzel became much interested in the beautifully illustrated paper by Istvánffi in which *Botrytis cinerea* is treated as the conidial condition of *Sclerotinia Fuckeliana*. As a critical reading of the paper showed him that Istvánffi had not actually demonstrated the connection between the two by means of cultures, he wished especially to be able to do so. In 1930, when in Switzerland, he collected a single apothecium growing from a sclerotium attached to a grape cane, and his studies indicated that it was that of *S. Fuckeliana*. Ascospore shootings made there from it gave a culture containing conidiophores and conidia of the *B. cinerea* type. Though he felt sure that he had *S. Fuckeliana*, he realized that his data were not conclusive. Nevertheless, due to the classical character of Istvánffi's work he expected to designate *S. Fuckeliana* the type species of *Botryotinia*. The very definite element of uncertainty involved in doing so and our desire to establish the genus on an unquestionably sound basis have led us to select *S. convoluta* Drayton (1937) instead. Type materials of all stages of this species have been preserved, the fungus was well known to Whetzel, and it has been carefully studied, fully described, and excellently illustrated.

Whetzel had obtained cultures of *Botrytis* of the *cinerea* type from many suscepts and had collected the apothecial condition in various cases. He planned to prepare a monograph of the species of *Botryotinia* and had placed tentative names on specimens in the herbarium indicating his intention to describe a half dozen or more new species.[7]

[7] In order to avoid publication of *nomina nuda* it has been necessary to refer to Professor Whetzel's undescribed material in this fashion. In the genera not yet monographed by him he expected to erect a considerable number of new species. The specimens on which these were to be based are preserved, with associated notes and photographs, in the herbarium of the Department of Plant Pathology of Cornell University, at Ithaca, New York. His studies of the various species were all as yet more or less incomplete. Specific diagnoses had not yet been prepared by him. Probably in time his materials will be incorporated in monographic studies by other students of the Discomycetes. An attempt on our part to include descriptive matter concerning these species in this synoptical paper would in any case be inappropriate.—It was Professor Whetzel's custom to obtain each species in pure culture on agar. The resulting collection of cultures was at times large, though he made no effort to maintain a complete set embracing all the

In connection with the discussion of this genus, reference should perhaps be made to *Sclerotinia polyblastis* Gregory (**1938**). This species, based on a genetic connection between *Botrytis polyblastis* Dowson (**1928**) and apothecial material described as its perfect stage, was apparently not seen by Whetzel in the living condition. As the *Botrytis,* with large conidia reaching 60 μ in diameter, is scarcely of the *cinerea* type, and as the structure of the sclerotium was not described, inclusion of this species in *Botryotinia* could not be more than tentative. Whetzel left no statement giving an indication of his viewpoint concerning its taxonomic status.

7. SEPTOTINIA Whetzel, Mycologia **29**: 134. 1937.

Stroma a circular to elongate or angular, thin, black sclerotium, maturing in the invaded tissues of the affected plant parts usually after they have fallen to the ground, digesting the available elements of the suscept and replacing them with a densely interwoven mass of hyphae among which resistant elements such as xylem vessels commonly persist; *medulla* structurally like that of *Botryotinia,* being composed of thin-walled hyphae embedded in a transparent, gelatinous to horny matrix; *spermidium* a minute spermodochium borne on the decaying tissues at the time of sclerotium formation; *spermatium* markedly ovate instead of globose, the basal end provided with a distinct stalk or collar; the gelatinous material in which the spermatia are embedded exceptionally persistent and tending to hold them together in long chains in which the stalks have the aspect of intercalary cells; *conidial fructification* a typical sporodochium composed of massed, branching, hyaline, septate conidiophores; *conidia* hyaline, elongate, typically one- or more-septate at maturity, extremely variable in length, attenuated above and with a truncate base; *apothecia* shallow cup-shaped, stipitate, arising from overwintered sclerotia which usually have become detached from the distintegrating suscept tissue and lie free in the soil or leaf mold; *asci* slender, cylindrical; *ascospores* hyaline,

species of the family. Having published on a species, the cultures involved were ordinarily discarded. After his death his assistant transferred all of his cultures to new tubes, but it is not planned to maintain them for any considerable period. Correspondents interested in obtaining cultures should request them at once.

ovoidal, non-septate; *paraphyses* simple or branched, with swollen tips.

Type species: *Septotinia podophyllina* Whetzel, Mycologia **29**: 135. *18 fig.* 1937.—*Syn. Gloeosporium podophyllinum* Ellis & Ev., Jour. Myc. **4**: 103. 1888, *Septogloeum podophyllinum* Sacc., Syll. Fung. **10**: 497. 1892.—This species occurs in the leaves and stalks of *Podophyllum peltatum* L. and is not known on other plants. The genus, as far as known to us, is monotypic. The above generic diagnosis is based wholly on Whetzel's published account of the genus. There, the type species is fully described and abundantly illustrated.

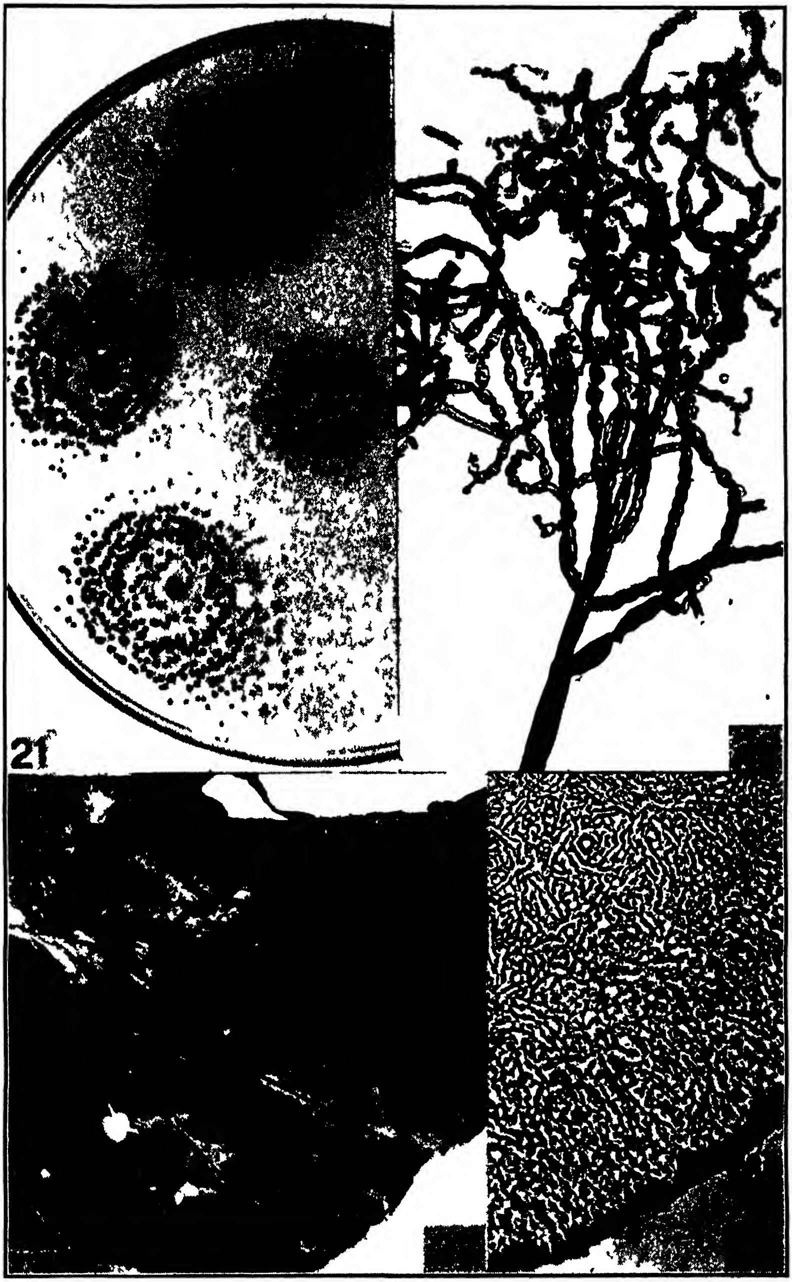
8. **Streptotinia** Whetzel, gen. nov.

(FIGS. 21–24)

Stroma a small, black sclerotium of the type here termed planoconvexoid, characteristically flattened loaf-shaped to hemispherical, firmly attached to the substrate and flat to concave on the attachment surface (FIG. 21), the rind being poorly developed or wanting there; *medulla* composed of narrow, thin-walled hyphae embedded in a hyaline, gelatinous matrix (FIG. 24); *spermatiophores* aggregated in spermodochia; *conidiophores* essentially as in *Botrytis* of the *cinerea* type except that the branches are strikingly and characteristically streptoform, *i.e.* twisted tightly as in *Streptothrix* (FIG. 22); *conidia* globose, smooth, hyaline or tinted; *apothecia* minute and short-stipitate; *ascospores* hyaline, unicellular, ellipsoidal; *generic characters* corresponding to those of *Botryotinia*, except in the streptoform nature of the branches of the conidiophore.

Apothecia sclerotiaque vere ut in *Botryotinia;* spermatia in spermodochiis sustenta; conidiophorae illarum *Botryotiniae* similes sed ramis notabile singulariterque streptoformibus, *i.e.* tortis; conidia laevia, hyalina vel leviter colorata.

FIGS. 21–24. *Streptotinia.* 21–23, *S. Arisaemae*, type species, *on Arisaema triphyllum.* 21, concentrically arranged loaf-shaped sclerotia resulting from conidial plantings on potato dextrose agar, Nat. size (*C8377 type specimen*). 22, conidiophore with typically twisted branches, × 180 (*C8377 type specimen*). 23, upper surface of leaf showing characteristic lesions, Nat. size (*C8250*). 24, *Botrytis Streptothrix* on *Orontium aquaticum,* structure of sclerotium as shown in free hand section, × 300 (*C8099*).

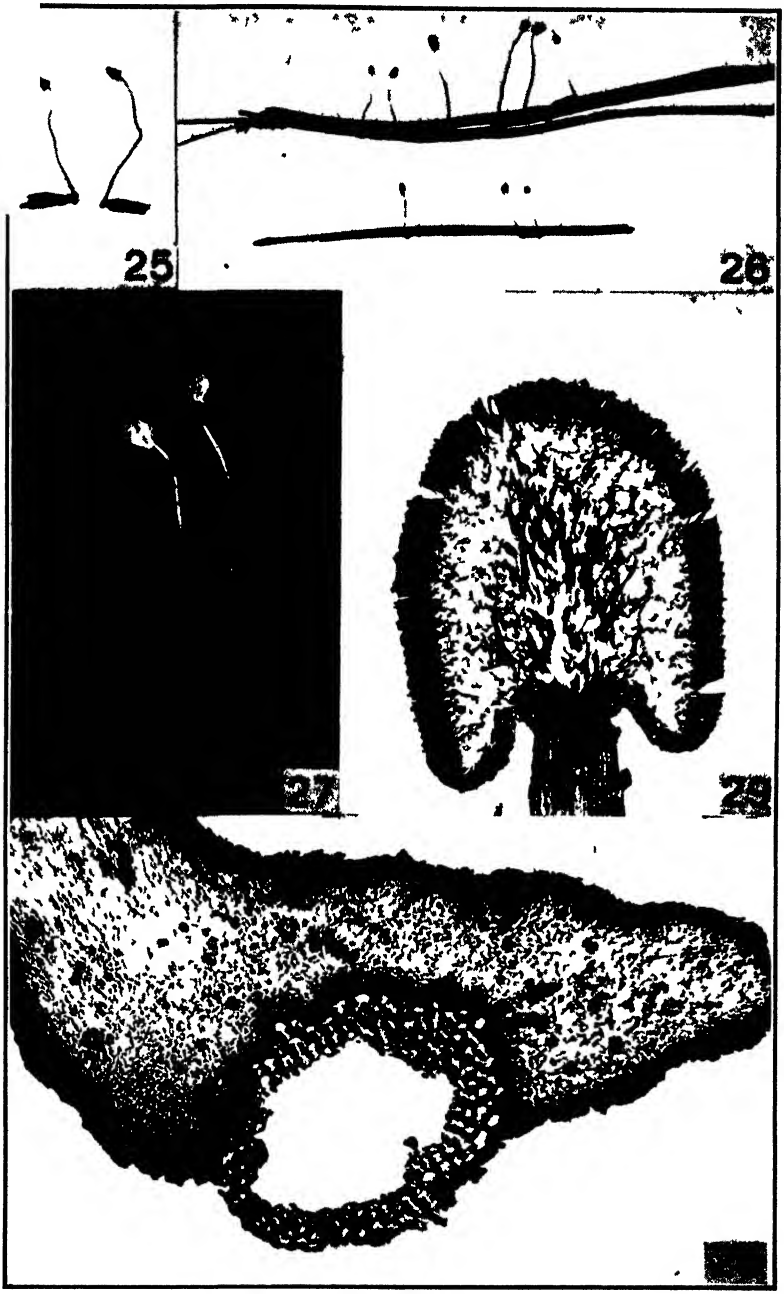


FIGS 21–24

Type species: Streptotinia Arisaemae Whetzel, sp. nov.—*Sclerotia* small to minute, chiefly not more than 0.5 mm. in diameter though sometimes twice that, loaf-shaped to hemispherical, smooth, shiny, round to oval or oblong or from coalescence somewhat irregular, in culture uniting rather characteristically in rows of three or more individuals but not tending to form crusts (FIG. 21); *conidiophores* scattered over the affected plant parts, arising singly or in small tufts which commonly merge to form a fluffy reddish-brown, discontinuous mat, dusty with conidia; the individual conidiophore composed of a long, slender, erect, cylindrical stalk and a rather broad, definitely terminal cluster of considerably narrower, interlacing, streptoform branches (FIG. 22); stalk about 1 mm. in length and approximately 25 μ in diameter, in reflected light noticeably iridescent; branches repeatedly forked and bearing botryose clusters of conidia on terminal branchlets; *conidia* globose, smooth, hyaline to tinted, mostly 6–7 μ in diameter; *apothecia* short-stalked, minute; the receptacle 1 mm. or less in diameter; *asci* 109–157 × 8–10 μ (mostly 130–150 × 9 μ), ascospores 8–14 × 4–6 μ (mostly 13 × 5 μ).

Sclerotia parva vel minuta, plerumque ne plus quam 0.5 mm. diametro, interdum bis tantum, subhemisphaerica vel hemisphaerica, laevia, nitida, globosa vel ovalia vel oblonga vel ex conjunctione aliquantum irregularia, haud crustas formantia; conidiophorae singulae vel in caespitibus parvis, plerumque mergentes, mattam rufo-fuscam intermittentem cum conidiis pulverulentam formantesque; singula conidiophora cum stipite longo, gracili, recto, septato, cylindracei, iridescenti, circa 1 mm. longo × 25 μ in diametro, cumque terminali aliquantum lato corymbo ramorum angustorum, tortorum, iterum iterumque furcatorum, in ramulis terminis botryoses conidiorum corymbos ferentiumque; conidia globosa, laevia, hyalina vel tingentia, plerumque 6–7 μ diametro; apothecia minuta, brevi-stipitata; cupula 1 mm.

FIGS. 25–29. *Verpatinia.* 25–28, *V. calthicola,* type species, on overwintered petioles of *Caltha palustris.* 25, long-stalked apothecia arising from detached portions of sclerotia, receptacle definitely campanulate, Nat. size (*C21996*). 26, sclerotia *in situ* giving rise to apothecia, Nat. size (*C25926 type specimen*). 27, pair of apothecia enlarged against black background to show the furrowed surface of the receptacle which in these individuals is subturbinate, × 2 (*C25926 type specimen*). 28, transverse section of long ribbon-shaped sclerotium lying lengthwise of the petiole between the cuticle and the underlying vascular bundles; sclerotium in this species avoiding incorporation of the bundles, × 85 (*C25926 type specimen*). 29, *Verpatinia* sp. collected on unidentified suscept at Tenaga, Quebec, longitudinal section of apothecial receptacle, × 120 (photo by D. B. O. Savile, loaned to us by F. L. Drayton).



FIGS. 25–29

minusve in diametro, asci 109–157 × 8–10 μ (plerumque 130–150 × 9 μ); ascosporae 8–14 × 4–6 μ (plerumque 13 × 5 μ).

Status conideus in foliis *Arisaemae triphylli* (L.) Schott. pathogenicus, apotheciis in sclerotiis in reliquiis foliorum hibernatorum formatis.

Whetzel's records indicate that he saw apothecia representing this genus only once. On that occasion he found them arising "in great numbers from numerous minute sclerotia all together on a largely disintegrated mass of leaf debris of *Arisaema triphyllum* (L.) Schott. Conidiophore tufts also arose from the sclerotia, apparently coming on after the apothecia were nearly gone." Cultures obtained from the conidia and ascospores were identical, in both cases forming sclerotia and conidiophores with characteristically twisted branches. Whetzel says in his notes: "This connection is, therefore, sure." The collection was made, May 19, 1927, at Labrador Lake, south of Syracuse, N. Y., near the village of Apulia. Unfortunately no photographs were obtained, and the apothecia were allowed to decay. Then all the material, apothecial, conidial, and sclerotial, was discarded. The cultures in time also disappeared. Though it was Whetzel's custom to obtain photographs of petri dish cultures and to preserve dried-down cultures as herbarium specimens, he did neither in this instance. No record of the collection remains, other than that embodied by him in his notes (*C31748*).[8] In them he gives measurements of apothecia, asci, ascospores, and conidia, and we have incorporated these in the above diagnosis. He does not provide adequate descriptive matter concerning the conidial or sclerotial stages.

Diseased leaves and stalks of *Arisaema triphyllum* (FIG. 23), bearing *Botrytis* conidiophores with characteristically streptoform branches, were collected by Whetzel and his students at a half dozen different stations in Central New York during the years 1915 to 1938. At various times cultures were made, and photographs of these showing sclerotia were taken. Desiccated cultures and photographs were preserved in the herbarium along with the collections of diseased plant tissue from which the isolations were

[8] The C preceding the accession number in this and other citations in this paper designates the herbarium of the Department of Plant Pathology of Cornell University, at Ithaca, New York.

made. These specimens were all regarded by Whetzel as representing a single species, and he considered the apothecial material, above described, to be its perfect stage. He applied the names *Botrytis Arisaemae* sp. nov. and *Streptotinia Arisaemae* sp. nov. to the specimens. Our description of the conidial and sclerotial stages in the above diagnosis is based on his specimens and photographs. We have selected one of the collections (*C8377*) as the *type material.* Though Whetzel failed to preserve apothecia of the species, it should be recalled that he emphasized repeatedly that in this group of Discomycetes apothecial characters usually have little if any value in taxonomic separations.

On a considerable number of occasions Whetzel and his associates collected *Botrytis* conidiophores with streptoform branches on diseased foliage and stems of various other suscepts in the region of Ithaca, N. Y. These embrace *Caulophyllum thalictroides* (L.) Michx., *Symplocarpus foetidus* (L.) Nutt., *Stylophorum diphyllum* (Michx.) Nutt., *Glaucium flavum* Crantz, and *Dicranostigma Franchettianum* Fedde. The material was believed by Whetzel to include several additional undescribed species of *Streptotinia,* and he placed tentative specific names on some of the specimens. In various instances cultures were made, and photographs of them were taken; but apothecial material was not encountered.

Whetzel wished to designate *Botrytis Streptothrix* (Cooke & Ellis) Sacc.[9] the type species of this genus, but neither he nor any other investigator, so far as known, ever saw apothecia of the species. In June, 1919, he collected conidial material (*C3099*) at Lakehurst, New Jersey, near the type locality, on living leaves of *Orontium aquaticum* L., the suscept from which the species was originally described. Cultures were obtained and photographs of these were taken. The conidiophores and sclerotia are very similar to those of *S. Arisaemae.* Considerable additional research must be done before certainty exists as to specific identities in the genus. Whetzel realized this and had hoped to complete a monograph of the genus before undertaking the present paper.

[9] Earlier named *Polyactis Streptothrix* Cooke & Ellis, Grevillea 7: 39. 1878, and distributed by Ellis, as N. Am. Fungi No. *130,* in the same year.

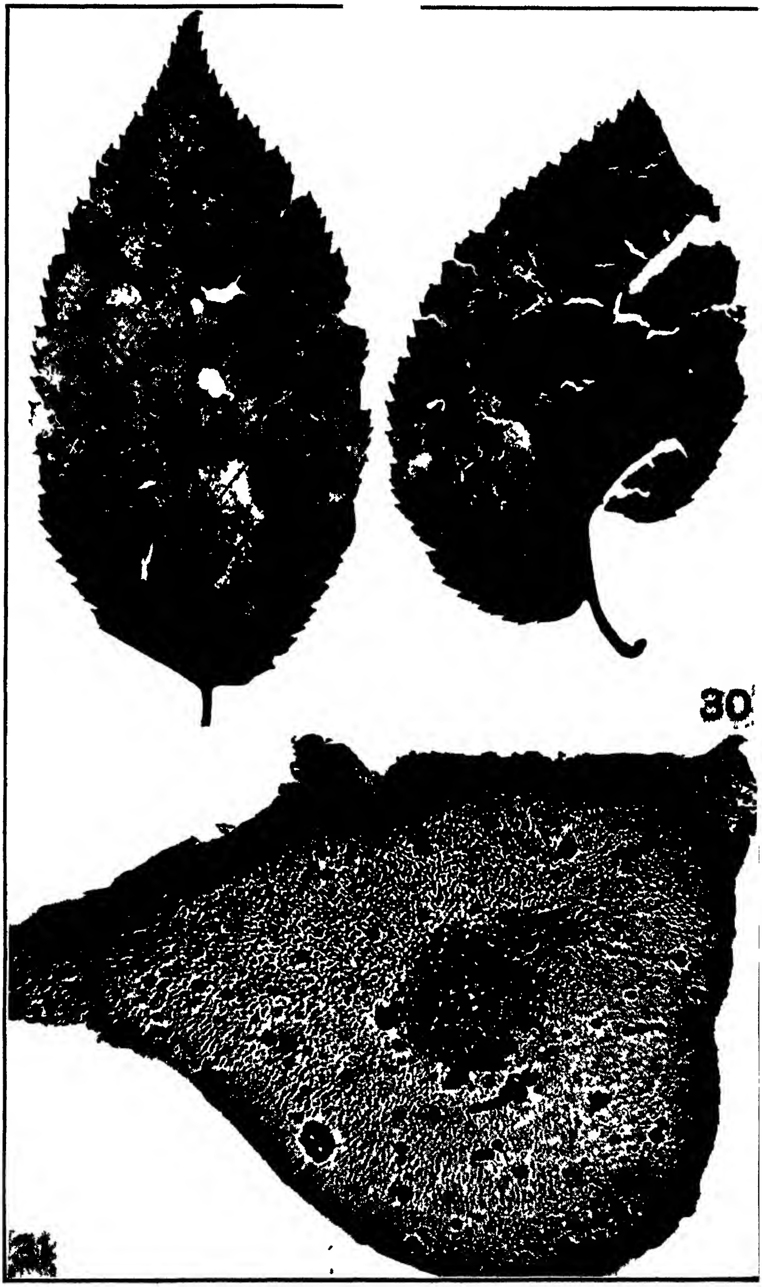
9. **Verpatinia** Whetzel & Drayton, gen. nov.

(FIGS. 25–31)

Stroma an elongate, black sclerotium of the discoid type, essentially identical with that of *Ciborinia*, foliicolous, formed beneath the cuticle, digesting the less resistant elements of the leaf tissue, and replacing them with a mass of densely interwoven hyphae, finally erumpent and more or less completely exposed but remaining partly embedded and germinating *in situ*, corresponding structurally with the tuberoid sclerotium of *Sclerotinia* but with undigested elements of the suscept tissue commonly persisting in the medulla; *rind* well differentiated and covering the sclerotium completely except at the places where undigested suscept elements such as vascular bundles protrude; *spermatia* not yet observed; *conidial stage* believed to be wanting; *apothecia* arising from the sclerotia singly or in pairs; *receptacle* characteristic, borne on a long, slender, delicate stipe and differing from that of the other genera of the family in being campanulate to cylindrical or subturbinate instead of cupulate to discoid (FIGS. 25–27); *hymenial surface* wrinkled or pitted, often more or less definitely longitudinally furrowed; tip of the stipe inserted considerably below the center of the receptacle, the margin of the latter hanging free (FIG. 29); neither stipe nor receptacle hollow, but the general form and aspect of the apothecium suggesting a tiny, long-stalked *Verpa; ascus* eight-spored, its tip thickened and staining blue with iodine; *ascospores* subbiseriate, hyaline, unicellular, ellipsoidal to fusiform, often with one side flat or slightly concave.

Stroma definitum sclerotium nigrum, in structura similis *Ciboriniae*, typice elongata, in tissibus folii formata, pro illis hyphas dense intertextas substituens, partibus elementorum resistentiorum manentibus; medulla intervallis inter hyphas dispersis, matrice gelatinosa deficiente; statibus spermatiis conideisque ignotis; receptaculum apothecii verpoideum, *i.e.* ut in *Verpa*, haud cupulatum, in stipite longo gracile sustentum; ascus octosporus, apice crasso cum iodini caeruleo tingente; ascosporae hyalinae, unicellulares, ellipsoideae vel fusiformes, saepe una parte planae vel aliquantum concavae.

FIGS. 30, 31. *Verpatinia duchesnayensis* on leaves of *Betula lutea*. 30, lower surface of leaf showing sclerotia in midrib and primary veins, Nat. size (*C28011*). 31, transverse section of sclerotium with central bundle of midrib embedded at its center; many other lesser elements of the suscept tissue especially of the palisade layer also embedded, × 85 (*C28011 type specimen*).



FIGS. 30, 31.

The apex of the columnar apothecial fundament, in its earliest stages, consists of a convex cushion bordered by an encircling roll or collar. The former is composed of tightly packed, parallel, vertical hyphae, the tips of which form the surface of the cushion and give it a papillate aspect. Their further elongation and branching results in enlargement of the end of the fundament to form the capitate, hymenium-covered receptacle. Meanwhile, the roll-like collar of bordering tissue, moving downward, becomes its pendent margin. This method of formation differs fundamentally from that of the cupulate receptacle of the other genera. Though in the genus *Coprotinia* the apothecium at maturity has the aspect of a minute, campanulate toadstool, careful observation shows the resemblance to that of *Verpatinia* to be merely superficial. The receptacle of *Coprotinia* in early stages is definitely cupulate, and the campanulate shape at maturity results from the pronounced recurving of its margin.

Type species: Verpatinia calthicola Whetzel, sp. nov.—*Sclerotium* narrow, ovate or oblong, tapering gradually to pointed ends, 3–10 mm. in length, usually about 1 mm. in width but occasionally twice that, forming a flat rather thin strip often not of uniform thickness running lengthwise in the cylinder of tissue composing the hollow petiole of the suscept and tending to avoid envelopment of its large vascular bundles (FIG. 28), either formed near the surface between the bundles and the cuticle and then at maturity so completely erumpent as to appear superficial, or lying deeper among the bundles, reaching the surface between them, and finally erumpent through one or more long slits in the tissue; persistence of undigested suscept elements in the medulla much less evident than in the following species; *exposed surface of the stroma* convex and marked by more or less prominent longitudinal striae or furrows; the opposite inner surface flat or concave; *fungus in culture* (on potato dextrose agar) forming a felty, gray, aerial, mycelial web bearing small, black, much fluted, irregular and anastomosing sclerotia; submerged mycelium brownish to black; *apothecial receptacle* campanulate to indefinitely turbinate (FIGS. 25–27), 2–3 mm. long, 1–2 mm. thick, clay color to sayal brown (Ridgway), terminating a long, slender, somewhat lighter-colored stipe; both with a tint of yellow; surface of receptacle

coarsely rugose, and marked with pits and furrows which often give a longitudinally ridged appearance (FIG. 27); *stipe* smooth, chiefly of uniform diameter throughout, sometimes swollen or flaring at the base, 5–15 mm. in length, approximately 0.5 mm. in diameter; *ascus* cylindrical in the upper spore-bearing half, tapering below very gradually to a rather broad base, 30–38 × 3–6 μ (chiefly 32 × 5–6 μ); *ascospores* ellipsoidal, with one side characteristically flat, 6–10 × 2–3 μ (chiefly 8 × 2.5 μ), becoming larger and irregular on germination, but remaining nonseptate.

Sclerotium in petiolo *Calthae palustris* L. formatum, angustum, ovatum oblongumve, acuta extrema versus gradatim conicum, plerumque circa 1 mm. latum, interdum bis tantum, 3–10 mm. longum, fasciam plana tenuem formans, saepe haud aequabiliter crassam, in longitudinem petioli in materia tubulati ejus cylindri currentem, fasces vasculares amplos haud involventem, vel prope superficiem externam inter fasces et cuticulam formatam, in statu adulto tote erumpentem per speciem externam, vel profundius inter fasces positam, superficiem inter illos per fissuras longas unas pluresve pervenientemque; in medulla persistentis indigestis tissuum elementis multo minus manifestis quam in specie secunda; superficies proposita stromae in longitudinem sulcata striatave; receptaculum apothecii campanulatum vel indefinite turbinatum, 2–3 mm. longum, 1–2 mm. crassum, argillaceum vel sayal fuscum (Ridgway), ad apicem stipiti longi, gracilis, magis leviter colorati; superficies receptaculi crasse rugosa cum foveis sulcisque; stipes laevis, per omnes partes in diametro praecipue constans, 5–15 mm. in longitudine, circa 0.5 mm. in diametro; ascus supra cylindratus, infra conicus, 30–38 × 3–6 μ (plerumque 32 × 5–6 μ); ascosporae ellipsoideae, uno lato applanatae, 6–10 × 2–3 μ (plerumque 8 × 2.5 μ), in germinatione amplificantes irregularesque sed nonseptata manentes.

This fungus was first collected by Whetzel, May 5, 1933, in the Lloyd-Cornell Reservation, near the village of McLean, fifteen miles northeast of Ithaca, New York. The apothecia were found arising from embedded sclerotia in overwintered petioles of *Caltha palustris* L. (*C21996*). He encountered the species again on overwintered petioles of the same host, May 23, 1937, near Labrador Lake, south of Syracuse, New York. On this occasion, material was collected more abundantly, full records were made, and photographs were obtained (*C25926, type specimen*). A third collection, possibly of this species, was made only two days later, May 25, 1937, at Tenaga, Quebec, Canada, by J. W. Groves and I. L. Conners. A portion of their material was submitted to Whetzel by F. L. Drayton, but the identity of the host was not de-

termined, and there is the possibility that the Canadian specimens represent another species of the genus. The coöperation of Dr. Drayton in this connection stimulated Professor Whetzel to share authorship of the genus with his well-known student and fellow-worker in the Discomycetes.

Verpatinia duchesnayensis Whetzel, sp. nov.—*Sclerotium* elongate, at maturity as much as 25 mm. in length though often much shorter, varying from short-fusiform in early stages to long, slender-cylindrical, with rather abruptly tapering, rounded to pointed ends, dull to shiny, formed in the midrib or one of the primary veins of the leaf (FIG. 30), digesting and replacing a section of it and at maturity attaining a thickness somewhat greater than that of the normal vein, commonly erumpent on both leaf surfaces but usually remaining firmly embedded and finally germinating *in situ,* in transverse section approximately triangular (FIG. 31), composed of densely interwoven hyphae among which undigested elements of suscept tissue are much more prominent than in the preceding species, enveloping the largely unaffected vascular bundle completely except at the ends where it protrudes through the black rind into the normal vein; *upper surface* of sclerotium flat or depressed, confined to the vein, or spreading laterally to a slight extent to form a thin, black, wing-like extension beneath the upper cuticle of the leaf blade; *lower surface* rounded like that of the normal vein and similarly marked, but with more prominent longitudinal wrinkles; *fungus in culture* (on potato dextrose agar) growing slowly and forming a chocolate-brown, much convoluted, flat, sclerotial mass, several centimeters in diameter, which darkens slowly to black; *apothecia* long-stalked, arising singly or in pairs from the embedded sclerotium; *receptacle* cylindrical to barrel-shaped or turbinate, approximately 2 mm. long, 1 mm. thick, pale ashy gray, surface deeply and irregularly furrowed or wrinkled; *stipe* of uniform diameter throughout, brownish, smooth, paler above, fibrillose at the base; *ascus* slender, cylindrical in the upper spore-bearing portion, tapering gradually toward the base and rather abruptly at the tip; *hymenium* containing peculiar, thick, apically swollen, paraphysis-like elements; *ascospores* fusoidal with one side often flat or slightly concave, 9.5–12 × 3–4 μ, swelling on

germination and forming a septate mycelium which tends to break up at the septa to form oidia of various lengths.

Sclerotium elongatum, ad 25 mm. longum, saepe multo brevius, quando juvenile breve fusiform, deinde longum gracile cylindratum, in diametro abrupte diminuens rotunda acuta extrema versus, in costa vel in vena primaria folii *Betulae luteae* Michx. f. formatum, sectionem illius digerens supplantansque, in statu adulto in diametro aliquantum majus quam vena, plerumque utrimque erumpidum sed in situ firme manens germinansque, sectione transversa circa triangulare; ex hyphis dense intertextis constructum, elementis indigestis prominentioribus quam specie typa, fasci vasculari tote involuto praeterquam extrema ubi fascis per corticem protrudit et in vena normali continuat; superioris sclerotii pagina plana saepe cum alis a latere subter cuticula superiore folii extentis; inferioris sclerotii pagina rotunda venae normalis similis cum rugis longitudinalibus prominentioribus; receptaculum apothecii cylindratum vel dolioforme vel turbinatum, circa 2 mm. longum × 1 mm. crassum, pallidum cinereum, superficie profunde irregulariterque sulcata, stipite in diametro per omnes partes uniforme, subfusco, laeve, supra pallidiore ad basim fibrilloso; ascus parte ascifera cylindratus, ad apicem abrupte conicus, infra gradatim conicus; ascosporae fusoidea, uno lato planae vel aliquantum concavae, 9.5–12 × 3–4 μ, in germinatione turgentes et formantes mycelium septatum ad septa saepissime frangens oidia longitudinibus variis formansque.

The apothecia of this species were collected by Whetzel, once only, August 23, 1938, near the Forest Rangers' School at the village of Duchesnay, in County Portneuf, Quebec, Canada, on the occasion of the sixth annual summer foray of the Mycological Society of America. They were found arising from embedded sclerotia in old, disintegrating, fallen leaves of *Betula lutea* Michx. f. (*C28011, type specimens* A & B, the latter a dried-down culture). Newly-fallen leaves of this host containing wholly similar sclerotia were collected later that season, Sept. 30 and Oct. 27, at the type locality at Whetzel's request by René Pomerleau (*C28011, type specimens* C & D respectively). In notes dealing with the first of these, written Oct. 14, Whetzel says: "In most of the leaves the sclerotia appear to be only partially developed; presumably their further development and growth occur after the leaves have fallen to the ground; for the most part the leaves sent were dead and brown, having recently fallen from the trees; in one case, however, the leaf was quite green and shows a young sclerotium on the midrib apparently developing beneath the epidermis." In notes written Oct. 31, concerning the second collection he states:

"Some of the leaves show distinct lighter-brown areas in which the sclerotia are formed. Some of these involve a third or a half of the leaf surface. These lighter-colored lesions indicate that the fungus kills the leaf tissue before the leaf falls. It is obvious to me that infection occurs while the leaves are still on the trees and that development of the fungus is probably very limited and not very injurious to the leaves until about the end of the season. On the other hand the fungus apparently does not spread widely through the tissues except about the immediate point of infection. The available material suggests that it is a typical necrogen." Though some of the leaves were placed outdoors over winter, additional apothecia were not obtained from the sclerotia the following summer, and, so far as known, other collections of the species have not been made.

10. OVULINIA Weiss, Phytopathology **30**: 242. 1940.

Stroma a thin, circular to oval or irregular, shallowly cupulate, black sclerotium, formed in the invaded suscept tissues but discrete at maturity and finally falling away; *rind* sharply differentiated and covering the whole sclerotium; *medulla* corresponding structurally to that of *Botryotinia*, the hyphae being embedded in a hyaline gelatinous matrix; the invaded suscept tissue so completely digested that remnants do not persist noticeably among the medullary hyphae; *spermatia* minute, globose, usually falling apart readily, but sometimes adhering in short chains, produced at the tips of short, fusoidal spermatiophores aggregated to form minute tufts or spermodochia on the surface of the suscept; *conidia* large, obovoid, unicellular except for a basal appendage consisting of a small, sterile disjunctor cell, hyaline, borne singly at the tips of short, simple branches of the mycelium which forms a mat on the surface of the invaded suscept tissue; *apothecia* of the *Sclerotinia* type, minute, arising singly or in small groups from the edge of the sclerotium; *asci* slender, cylindrical, 8-spored; *ascospores* ellipsoidal, unicellular, hyaline, typically uniseriate; *paraphyses* chiefly unbranched, septate, terete with swollen tips.

Type species: *Ovulinia Azaleae* Weiss, Phytopathology **30**: 243. 1940.—This species forms its sclerotia in the tissue of the

corolla of cultivated azaleas and rhododendrons, causing a destructive flower blight in the southern United States. Under experimentally controlled conditions it has proved pathogenic on *Kalmia* and *Vaccinium* also. The genus, as far as known, is monotypic. The above diagnosis is based on the original publication of Weiss, and on our own examination of thin sections of sclerotia.

11. COPROTINIA Whetzel, Farlowia **1**: 484. 1944.

Stroma not yet observed in nature, as developed on potato dextrose agar of indefinite form, black, 1–2 mm. thick, differentiated into rind and medulla and in structure very similar to the sclerotium of *Botryotinia*; *rind* formed above or beneath the surface of the medium, composed of one to several layers of densely interwoven, slender hyphae, dark-brown to black; *medulla* of rather closely interwoven, slender, thin-walled hyphae embedded in a rubbery transparent matrix; *spermidia* not observed; *conidial stage* regarded as wanting; *apothecia* gregarious, some shade of brown, extremely long- and slender-stipitate; *receptacle* small, thin, at first cupulate but with the margin so strongly recurved at maturity that the appearance of a tiny toadstool is assumed; *stipe* hair-like, its surface adorned with scattered, glandular hyphal tips; *asci* very small, clavate, tapering gradually to the base; apex thickened; pore plug colored faintly blue with iodine; *ascospores* minute, slender-ellipsoidal, unicellular, hyaline; *paraphyses* cylindrical and thin-walled.

Type species: *Coprotinia minutula* Whetzel, Farlowia **1**: 484. 1944.—Collected only once on a small dung-ball of some unidentified animal at Malloryville, New York, June 22, 1942. This species and *Martinia panamaensis* Whetzel are the only known coprophilous species of the Sclerotiniaceae. The genus *Coprotinia*, as far as known, is monotypic. The above diagnosis is based wholly on Whetzel's original description.

12. MARTINIA Whetzel, Mycologia **34**: 585. 1942.

Stroma a minute, hemispherical, black sclerotium, of the planoconvexoid type, firmly attached to the substratum, flat on the attachment surface. 1–2 mm. in diameter. often fusing with neigh-

boring sclerotia to form small lobular aggregations; *rind* and *medulla* structurally as in *Botryotinia*; *spermatia* known only in culture, globose, produced from the ends of Indian-club shaped spermatiophores borne on the aerial mycelium in naked fascicles (spermodochia); *conidial stage* regarded as wanting; *apothecia* small, white, thin, membranous, fragile, rather long-stalked; *receptacle* saucer-shaped to flat-expanded; *hymenial disc* at the maturity of the ascospores olivaceous to smoky brown, becoming immediately lighter colored on spore discharge; *asci* minute, 8-spored; *ascospores* unicellular, biguttulate, ellipsoidal, olive brown; *paraphyses* few, appearing simple, but actually forked near the base, slender, cylindrical, apically almost imperceptibly enlarged.

Type species: *Martinia panamaensis* Whetzel, Mycologia **34**: 586. 1942.—This species has unusually small asci and ascospores as compared with those of species in related genera having equally small apothecia. The species is known from two collections made in Panama and the Canal Zone, in 1935 and 1937 respectively, from bark or wood of rotten logs and branches of unidentified trees. A third collection, apparently of the same species, was made in the summer of 1938 near Quebec, Canada. In this instance the apothecia developed in the laboratory from a ball of rabbit dung brought in from the open. This is especially interesting since a coprophilous tendency has been noted nowhere else in the family except in the single known collection of *Coprotinia minutula* Whetzel. The genus *Martinia* is the only member of the Sclerotiniaceae in which distinct sclerotia and brown ascospores occur together. Our treatment of this genus is based wholly on Whetzel's original description. Additional species are not known to have been described.

13. RUTSTROEMIA Karsten emend. Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. III. 763. 1893; see White, W. L., Lloydia **4**: 169. 1941.

Stroma sometimes of doubtful occurrence or rudimentary, usually definitely present but indeterminate in extent and of the type here designated substratal, not a definite sclerotium, consisting of a stromatized portion of the substrate blocked off by, manteled

by, or more or less surrounded by a thin, black rind of fungus cells; *rind* thin, carbonaceous, composed of small, irregularly isodiametric cells, effuse on the surface of woody and other substrata, occurring as a thin black line or band in leaf tissues, or forming a cylinder surrounding petioles, veins, etc., always originating beneath the surface of the substrate and becoming superficial through sloughing off of the outer layer of tissue; *medulla* often indefinite in extent, but composed as in *Lambertella* of partially digested elements of the substrate threaded through and through with thin-walled, hyaline, branching hyphae; similar stromata formed in agar cultures; *spermogonia* minute, black, lenticular, solitary, subcuticular, rupturing irregularly, associated with and often adjacent to or confluent with the stroma, but always seated directly on the substrate; *spermatiophores* borne in a palisade layer on the basal wall of the spermogonium, in agar cultures arising singly from vegetative hyphae or forming a palisade layer in an acervulus-like depression in the stroma, often present in abortive form as minute tubules protruded by the ascospore at late maturity; *spermatia* broadly ellipsoidal to subglobose; *conidial stage* wanting; *apothecia* characteristically produced in late summer and early autumn, short- to long-stalked, typically brown, rarely yellow, greenish yellow, dark green, or white, firmly waxy-coriaceous, becoming hard and darker on drying, of complex structure, usually entirely prosenchymatous with a middle gelatinous zone in the ectal excipulum; *ascospores* usually large, hyaline, narrowly ellipsoidal to oblong or reniform, unicellular, sometimes becoming 2–6-celled at late maturity.

This diagnosis is based largely on that provided by White (1941) in his monographic treatment of this genus, but incorporates Whetzel's fundamentally different viewpoint concerning the nature of the stroma. Statements in Whetzel's notes indicate clearly that he regarded the stroma in this genus as corresponding in its essential features to that of *Lambertella* and considered the "carbonaceous black stroma" of White to be merely the rind.

White included twenty species in *Rutstroemia* and considered that they form a natural taxonomic unit. He enumerated seven characters which seemed to him the most fundamental features of the genus. No one of these is infallibly common to all the species,

a combination of any five of them being regarded by him as adequate basis for incorporation of a species in the genus. This results in a wider range and a greater diversity of form than is encountered in any other genus of the family.

Type species: *Rutstroemia firma* (Pers. ex Fries) Karsten, Bidr. Finl. Nat. Folk **19**: 108. 1871.—*Syn. Peziza firma* Pers., Syn. Fung. p. 658. 1801.

Included species:

R. americana (Durand) White, Lloydia **4**: 188. 1941.—*Syn. Ciboria americana* Durand, Bull. Torrey Club **29**: 461. 1902.

R. bolaris (Batsch ex Fries) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 765. 1893.—*Syn. Peziza bolaris* Fries, Syst. Myc. **2**: 112. 1822.

R. calopus (Fries) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 768. 1893.—*Syn. Peziza calopus* Fries, Obs. Myc. **2**: 307. 1818; Syst. Myc. **2**: 131. 1822.

R. echinophila (Bull. ex Fries) von Höhnel, Sitzungsber. Akad. Wiss. Wien, I Abt. **126**: 340. 1917.—*Syn. Peziza echinophila* Fries, Syst. Myc. **2**: 118. 1822.

R. elatina (Alb. & Schw. ex Fries) Rehm, *in* Rabenh. Krypt.-Fl. Deutschl. **1**: Abt. 3. 767. 1893.—*Syn. Peziza elatina* Fries, Syst. Myc. **2**: 112. 1822.

R. longiasca (Cavara) White, Lloydia **4**: 195. 1941.—*Syn. Pyrenopeziza longiasca* Cavara, Rev. Myc. **11**: 178. 1889.

R. longipes (Cooke & Peck) White, Lloydia **4**: 203. 1941.—*Syn. Peziza longipes* Cooke & Peck, Buffalo Soc. Nat. Sci. p. 295. March, 1875.

R. luteo-virescens (Roberge) White, Lloydia **4**: 211. 1941.—*Syn. Peziza luteo-virescens* Roberge, *in* Desmaz. Pl. Crypt. Fl. fasc. 31. No. *1541*. 1846; Ann. Sci. Nat. III. **8**: 188. 1847.

R. macrospora (Peck) Kanouse apud Wehmeyer, Canad. Jour. Res. **18**: 547. 1940.—*Syn. Helotium macrosporum* Peck, Ann. Rept. New York State Museum **26**: 82. 1874.

R. Nerii Whetzel & White, Lloydia **4**: 226. 1941.

R. nervisequa (Schröt.) White, Lloydia **4**: 223. 1941.—*Syn.*

Sclerotium nervale Alb. & Schw., Consp. Fung. p. 64. 1805, *Sclerotinia nervisequa* Schröt., Krypt.-Fl. Schl. **3**: 65. 1893.

R. petiolorum (Roberge) White, Lloydia **4**: 197. 1941.—*Syn. Peziza petiolorum* Roberge, *in* Desmaz. Pl. Crypt. Fl. ed. 1. No. *1158*. 1842; Ann. Sci. Nat. II. **17**: 96. 1842.

R. Poluninii Linder, Lloydia **4**: 224. 1941.

R. Pruni-serotinae Whetzel & White, Lloydia **4**: 219. 1941.

R. Pruni-spinosae (Libert) Whetzel & White, Lloydia **4**: 219. 1941.—*Syn. Sclerotinia Pruni-spinosae* Lib. ex Speg. & Roum., *in* Roum. Fungi Sel. Gall. Exs. No. *642*. 1880; *in* Saccardo, Michelia **2**: 328. 1881.

R. renispora (Ellis) White, Lloydia **4**: 215. 1941.—*Syn. Helotium renisporum* Ellis, *in* Cooke, Bull. Buffalo Soc. Nat. Sci. p. 299. March, 1875.

R. setulata (Dearn. & House) White, Lloydia **4**: 193. 1941.—*Syn. Ombrophila setulata* Dearn. & House, Ann. Rept. New York State Museum **1924**: 60. 1925.

R. Sydowiana (Rehm) White, Lloydia **4**: 200. 1941.—*Syn. Ombrophila Sydowiana* Rehm, *in* Sydow, Myc. March. No. *666*. 1884, *Ciboria Sydowiana* Rehm, Hedwigia **24**: 226. 1885.

R. urceolus (Fuckel) White, Lloydia **4**: 194. 1941.—*Syn. Patellaria urceolus* Fuckel, Symb. Myc. Nachtr. **2**: 54. 1873.

The above species are those placed in the genus by White. Whetzel had a manuscript in preparation in which he hoped to publish eight or ten additional species in co-authorship with White.

14. LAMBERTELLA von Höhnel, Sitz. Akad. Wiss. Wien I. Abt. **127**: 375. 1918.

Stroma diffuse, indeterminate, of the type here designated substratal, not a definite sclerotium, consisting of a stromatized portion of suscept tissue blocked off by or completely surrounded by a thin black rind of fungus cells; *rind* composed of a single layer of dark-colored, thick-walled cells which present a striking and characteristic pattern in surface view, there being a narrow translucent line between the contiguous walls of adjacent cells; *medulla* composed of partially digested suscept elements interlaced through and

through with a loose network of repeatedly branching, anastomosing, thin-walled, hyaline, septate hyphae; the fungus hyphae and suscept elements apparently enveloped together in a transparent, gelatinous matrix in which they are somehow preserved from decay until the food thus stored in the stroma is finally used in apothecial formation; *spermatia* globose to slightly elliptical, hyaline, produced successively from the tips of clavate spermatiophores borne in fasciculate naked spermodochia or in covered lenticular, black, spermogonia; *conidial stage* wanting; *apothecia* stipitate, arising from the stromatized substrate and firmly attached to it, scattered to gregarious, fleshy, elastic, becoming coriaceous or corneous on drying, reviving when moistened, usually some shade of vinaceous brown (Ridgway) or, when fresh, yellowish brown; *receptacle* cup-shaped or shallow saucer-shaped to applanate when mature; hymenial disc strikingly darker just before spore discharge, lighter immediately afterward; *stipe* relatively stout, variable in length, sometimes apparently wanting, concolorous with the receptacle, puberulent, hirsute or furfuraceous, fibrillose; *asci* usually stout-cylindrical to clavate, attenuated below, rounded to truncate and thickened at the tip which has a prominent pore plug staining blue with iodine, 8-spored; *ascospores* one-celled, broadly ellipsoidal, ovoidal, or lunate, usually flattened or concave on one face, the opposite convex wall being more or less thickened, strikingly biguttulate when young, smooth or roughened, golden brown or, when fully mature, olivaceous brown, uniseriate, tending to become biseriate before discharge; *paraphyses* two- to three-branched, slender, septate, hyaline; the terminal cell usually somewhat clavate.

In leaf-inhabiting species of the genus the stromatized block of tissue is usually delimited by a narrow black band of rind cells passing through the leaf tissues perpendicular to the surface. The rind may or may not extend partially over the surfaces of this blocked off portion. In fruit-inhabiting species the rind covers the entire surface of a thin peripheral layer or shell of stromatized suscept tissue surrounding the non-stromatized tissues of the fleshy part of the fruit and the enclosed seed. The stroma differs fundamentally in character from that of *Monilinia* where a similar peripheral stromatic shell exists but is structurally of the tuberoid type. In *Monilinia* the medulla is composed of tightly inter-

woven, thick-walled hyphae, and is covered on the inner surface as well as the outer with a fully differentiated rind. The genus *Martinia,* the only other genus of the family having colored ascospores, differs from *Lambertella* in forming a definite sclerotium. This discussion and the above diagnosis are based wholly on the statements published by Whetzel (**1943**) in his monographic treatment of this genus. There greater detail and adequate illustrations are provided.

Type species: *Lambertella Corni-maris* von Höhnel, Sitz. Akad. Wiss. Wien, I. Abt. **127**: 375. 1918.

Included species:

L. Cephalanthi Whetzel, Lloydia **6**: 47. 1943.
L. colombiana Cash & Whetzel, Lloydia **6**: 51. 1943.
L. Hicoriae Whetzel, Lloydia **6**: 33. 1943.
L. Jasmini Seaver & Whetzel, Lloydia **6**: 37. 1943.
L. Pruni Whetzel & Zeller, Lloydia **6**: 40. 1943.
L. tropicalis (Kanouse) Whetzel, Lloydia **6**: 49. 1943.—*Syn.* *Ciboria tropicalis* Kanouse, Mycologia **33**: 463. 1941.
L. Viburni Whetzel, Lloydia **6**: 43. 1943.

15. **Seaverinia** Whetzel, gen. nov.

(FIGS. 32–36)

Stroma of the type here designated substratal, poorly developed, perhaps vestigial, not a definite sclerotium, formed in the rhizome of the suscept and visible on its surface usually as a narrow black line formed of typical rind cells where the hyphal mass bursts through the peripheral cork layer, in some cases emergent over a wider, less elongate area to form a small black patch (FIG. 35); *medulla* filling a more or less superficial cavity in the suscept tissue, commonly a long, narrow, shallow crevice, and consequently appearing broadly wedge-shaped in transverse section, composed of loosely interwoven, thin-walled hyphae mixed with partially digested elements of the suscept tissue; stromatal hyphae richly connected to hyphal ramifications which are evident throughout the adjacent invaded tissue of the rhizome; this suscept tissue rotted

FIGS 32, 33. *Seaverinia Geranii*, type species, on *Geranium maculatum* 32, partially exposed rhizomes bearing apothecia, photographed in their natural position in the soil. 33, apothecia attached to rhizomes and roots removed from the soil, Nat. size (*C21988*).

to a dry mealy consistency and of a characteristically reddish-brown color, many of its cells retaining their form, but their walls abnormally thickened and yellowed; *spermatia* not observed; *conidial stage* placed originally in the form-genus *Botrytis* by Seaver and Horne but excluded from it by Whetzel chiefly because the conidia differ from those of *Botrytis* of the *cinerea* type in being tuberculate and because the apothecium does not arise from a true sclerotium; *conidiophores* botryose, 1 mm. or more in length, pale-brown, sparsely septate, formed in tufts on the rhizome and roots of the suscept, and under moist conditions profusely developed, bearing conidia in rather dense clusters; *conidia* unicellular, pale-brown by transmitted light, minutely but definitely tuberculate, subglobose, tapering somewhat to the point of attachment, slightly longer than broad; *apothecia* arising from the partially decayed rhizome in clusters of varying number, stipitate; the length of the stipe varying considerably and dependent in part on the depth to which the rhizome is buried; *receptacle* shallow cupulate to subdiscoid, reaching a diameter of 15 mm.; *asci* cylindrical in the spore-bearing portion, tapering above and below, 8-spored; *ascospores* hyaline, ellipsoidal, unicellular.

Stroma in typo substratea, haud sclerotium definitum, male formata, interdum vestigialis, in rhizoma *Geranii maculati* L. formata et in superficie sua manifesta plerumque per lineam angustam nigram ex cellis typicis cuticis formatam ubi massa hyphorum per corticem peripheralem perrumpet, interdum in area latiore minus elongata emergens, maculam parvam nigram formans; medulla cavum plus minusve superficiale plerumque riman longam angustam tenuem complens, propterea in sectione transversa late cuneata vel tuberculiformis, ex hyphis parietibus tenuibus laxe intertextis et ex elementis aliquatenus digestis tissuum rhizomae composita; spermatia non observata; status conideus *Botrytitis* typi *cinerei* similis sed conidia tuberculata; apothecia ex rhizomis aliquatenus putribus et plus minusve definite ex stromata oriunda, forma, modo, coloreque eorum *Sclerotiniae* vere similia, receptaculo tenui-cupulato vel subdiscoideo; asci clavaformi-cylindrati octo-sporati; ascosporae hyalinae, ellipsoideae, unicellulares.

Type species: Seaverinia Geranii (Seaver & Horne) Whetzel, comb. nov.—*Syn. Sclerotinia* (*Stromatinia*) *Geranii* Seaver & Horne, Memoirs Torrey Club **17**: 205–206. 1918.—The species is known only from the rhizomes of *Geranium maculatum* L., the type locality being the northern end of Van Cortlandt Park, New York City. It has also been found on the grounds of the New

FIGS. 34–36.

York Botanical Garden in Bronx Park. Davis (1926) reported its occurrence near Madison, Wisconsin. The genus, as far as known, is monotypic.

Whetzel collected the species twice, May 1, 1919 and April 22, 1927, at the type location in the company of Seaver. Later he found it on several occasions in considerable quantity in the Lloyd-Cornell Reservation at McLean, New York, near Ithaca (FIGS. 32, 33). He studied the fungus in cultures obtained from single ascospores and conidia. Definite sclerotia such as those of *Botryotinia* did not develop (FIG. 36). The above description of the stroma was based by us on his notes and photographs and on our own study of sectioned rhizomes. One of the sections examined (FIG. 34) shows the base of a tuft of conidiophores attached to the surface of the stroma. Though Whetzel was undoubtedly convinced that the stroma is that of *S. Geranii*, and presumably performed experiments demonstrating the point to his own satisfaction, we have failed to find records in his notes in this connection.

INDEX TO SPECIES

New names and combinations are in boldface, synonyms in italics

FIGS. 34–36. *Seaverinia Geranii* on *Geranium maculatum*. 34, stroma in transverse section; at the top of the photograph the base of a cluster of conidiophores arising from the rind is shown, × 85 (*C21988*). 35, stromata visible as prominent black lines and patches on the surface of the rhizome, × 3 (*C21988*). 36, original petri dish culture obtained by blowing conidia over the surface of the agar; though conidiophores cover much of the mycelium, definite sclerotia lacking, Nat. size (*C10781*).

GENERIC HOST INDEX OF SCLEROTINIACEAE LISTED IN THIS PAPER [10]

ABIES—*Rutstroemia elatina.*

ACER—*Ciboria acerina, Rutstroemia luteo-virescens, R. macrospora, R. setulata, ?R. Sydowiana.*

ALLIUM—*Botryotinia Porri, Stromatinia cepivorum.*

ALNUS—*Ciboria Alni, C. amentacea, Rutstroemia firma, R. nervisequa.*

AMELANCHIER—*Monilinia Amelanchieris, M. Johnsonii.*

APIUM—*Sclerotinia minor.*

ARISAEMA—*Streptotinia Arisaemae.*

AZALEA—*Monilinia Azaleae, Ovulinia Azaleae.*

BETULA—*Ciboria Betulae, Rutstroemia firma, R. macrospora, R. petiolorum, Verpatinia duchesnayensis.*

CALTHA—*Verpatinia calthicola.*

CAMELLIA—*Sclerotinia Camelliae.*

CAREX—*Ciboria Aschersoniana, Sclerotinia Caricis-ampullaceae, S. Duriaeana, S. longisclerotialis, S. sulcata.*

CARPINUS—*Ciboria Carpini, Rutstroemia bolaris, R. firma.*

CARYA—*Lambertella Hicoriae.*

CASTANEA—*Ciborinia Candolleana, Rutstroemia americana, R. echinophila, ?R. petiolorum.*

CEPHALANTHUS—*Lambertella Cephalanthi.*

CITHAREXYLUM—*Lambertella Jasmini.*

COCCOLOBIS—*Lambertella tropicalis.*

CORNUS—*Lambertella Corni-maris, Monilinia Corni.*

CORYLUS—*Ciboria Coryli, Rutstroemia bolaris, R. firma.*

CRATAEGUS—*Monilinia Johnsonii, Rutstroemia Pruni-spinosae.*

CROCUS—*Stromatinia Gladioli.*

CYDONIA—*Monilinia Cydoniae.*

DAUCUS—*Sclerotinia intermedia.*

EQUISETUM—*Rutstroemia Poluninii.*

ERIOBOTRYA—*Lambertella Jasmini.*

ERIOPHORUM—*Sclerotinia Vahliana.*

ERYTHRONIUM—*Ciborinia Erythronii, C. gracilis.*

FAGUS—*Rutstroemia bolaris, R. macrospora, R. petiolorum.*

FRAXINUS—*Rutstroemia macrospora, R. longipes.*

FREESIA—*Stromatinia Gladioli.*

GERANIUM—*Seaverinia Geranii.*

GLADIOLUS—*Stromatinia Gladioli.*

HUMULUS—*Rutstroemia bolaris.*

IRIS—*Botryotinia convoluta.*

JASMINUM—*Lambertella Jasmini.*

JUGLANS—*Rutstroemia macrospora.*

JUNCUS—*Sclerotinia Curreyana.*

[10] This index, submitted by Dr. J. Walton Groves for insertion in the paper, does not include the recorded suscepts of the omnivorous species, *Sclerotinia sclerotiorum,* nor does it, of course, embrace those of Whetzel's as yet unpublished new species. It should be noted too that not all the described species of the Sclerotiniaceae are listed in this paper.

KALMIA—*Ovulinia Azaleae* (artificial infection).
LACTUCA—*Sclerotinia minor.*
LAPEIROUSIA—*Stromatinia Gladioli.*
LEDUM—*Monilinia Ledi.*
LIGUSTRUM—*Rutstroemia Pruni-spinosae.*
MELILOTUS—*Sclerotinia sativa.*
MESPILUM—*Monilinia Mespili.*
MORUS—*Ciboria carunculoides, C. Shiraiana.*
MYRICA—*Ciboria acerina.*
NARCISSUS—*Sclerotinia sativa.*
NERIUM—*Rutstroemia Nerii.*
NYSSA—*Rutstroemia macrospora, R. renispora.*
OSTRYA—*Ciboria acerina.*
PANAX—*Sclerotinia Panacis, Stromatinia Smilacinae.*
PARIS- *Stromatinia Paridis.*
PLATANUS—*Rutstroemia luteo-virescens.*
POA—*Rutstroemia calopus.*
PODOPHYLLUM—*Septotinia podophyllina.*
POLYCODIUM—*Monilinia Polycodii.*
POPULUS—*Ciboria Caucus, Ciborinia bifrons, C. confundens, Rutstroemia firma, R. nervisequa.*
PRUNUS—*Lambertella Pruni, Monilinia demissa, M. fructicola, M. fructigena, M. laxa, M. Padi, M. Seaveri, Rutstroemia Pruni-serotinae, R. Pruni-spinosae.*
PYRUS—*Monilinia Johnsonii, M. megalospora.*
QUERCUS—*Ciborinia Candolleana, Rutstroemia bolaris, R. echinophila, R. firma, R. macrospora, R. petiolorum, R. Sydowiana.*
RHODODENDRON—*Monilinia Azaleae, M. Rhododendri, Ovulinia Azaleae.*
RIBES—*Rutstroemia firma.*
RICINUS—*Botryotinia Ricini.*
ROSA—*Rutstroemia longiasca.*
RUBUS—*Rutstroemia firma, R. urceolus.*
SALIX—*Ciboria acerina, C. amentacea, C. amenti, C. Caucus, Ciborinia foliicola, Rutstroemia bolaris.*
SCIRPUS—*Sclerotinia scirpicola.*
SMILACINA—*Stromatinia Smilacinae.*
SORBUS—*Monilinia Ariae.*
TILIA—*Rutstroemia luteo-virescens.*
TRAGOPOGON—*Sclerotinia intermedia.*
TRIFOLIUM—*Sclerotinia Trifoliorum.*
TRITONIA—*Stromatinia Gladioli.*
TSUGA—*?Rutstroemia elatina.*
TULIPA—*Sclerotinia sativa.*
ULMUS—*Rutstroemia firma.*
VACCINIUM—*Monilinia baccarum, M. Ledi, M. megalospora, M. Oxycocci, M. Urnula, M. Vaccinii-corymbosi, Ovulinia Azaleae* (artificial infection).
VIBURNUM—*Lambertella Viburni.*
VITIS—*Sclerotinia Fuckeliana.*

MISCELLANEOUS SUBSTRATA

DUNG—*Coprotinia minutula, Martinia panamaensis.*
GROUND—*Stromatinia Rapulum.*
NUT—*Lambertella columbiana.*
WOOD—*Martinia panamaensis.*

DEPARTMENT OF PLANT PATHOLOGY,
CORNELL UNIVERSITY,
ITHACA, NEW YORK

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SPECIES OF SYNCHYTRIUM IN LOUISIANA. III. THE DEVELOPMENT AND STRUCTURE OF THE GALLS

MELVILLE T. COOK

(WITH 12 FIGURES)

The fungi belonging to this genus consist, in the vegetative stage, of a single cell, living as a parasite in a single cell of a higher plant. The infections so far as known are by means of zoöspores, and are in cells that are not fully mature but cells of slightly different ages in the same leaf may be infected. After infection the fungus grows rapidly, the host cell enlarges, and usually a gall is formed by the growth of the surrounding host cells. The zoöspores are transparent and so small that they are easily overlooked. After the zoospores penetrate the host cell the fungus grows, becomes pale yellow, then deep yellow, and finally in some species orange or red. The fungus has a very large nucleus but this will not be discussed in this paper. The wall which forms around the fungus very early consists, in many and possibly all species, of three layers; the inner and middle layers are formed by the fungus, while the outer is formed from the disintegrating contents of the host cell. The thickness of the wall varies in different species and with age. It is usually thin at maturity. The inner and middle layers may be so closely united that it is difficult to determine whether there are one or two layers. The outer layer may be prominent or reduced to a few granules. The fungus grows to full size and then segments by the formation of septa which originate at the periphery, grow inward and separate the body into sporangia. The number of sporangia formed from a single infection is variable and of very little value in descriptions and for determination of species. Pronounced variations in number and size may be found in a single infected leaf. Each sporangium contains a single nucleus which divides into many, each becoming the center of a zoöspore. In some species there appears to be a single generation; the sporangia

persisting in some unknown manner until the following year when the zoöspores appear and infect young plants. Other species have several generations, each producing zoöspores that infect plants and then a generation which carries the plant to the following year.

The life histories of a few species have been studied but very little attention has been given to the structures of the galls in which the fungi develop. These gall structures appear to be more characteristic and more satisfactory for determinations and descriptions than the characters of the fungi. It is the purpose of this paper to describe the structure and development of these galls, although some attention will be given to the development of the fungi. The infections in all species described in this paper are in the epidermal cells, mostly in the leaves before they are fully developed. A few workers have reported sub-epidermal infections but some of these records are doubtful. The infected host cell grows rapidly and in most cases is almost or completely filled by the fungus early in its development. The relative sizes of fungus and host cell depend on age. The nucleus of the infected cell persists for a time but disappears before the formation of the sporangia; the protoplasm undergoes disintegration, some of it going to the formation of the outer layer of the wall around the fungus, which is abundant in some species and sparse in other species.

The fungus stimulates the growth of the cell in which it lives and also some of the surrounding cells of the host plant. The epidermal cells in contact with the infected cell grow in such a manner as to partly or completely cover it, depending on the species of the fungus. In some species the other surrounding host cells, especially those in contact with the infected cell, also grow and form a definite and characteristic sheath. These growths of the host cells result in the formation of a gall with distinctive characters by which the species of the fungus can be determined. In most species the gall is partly submerged in the tissues of the host; in some few species it is completely embedded and in other species rests on the surface of the host plant. Although the infected cell may be partly or completely embedded in the tissues of the host plant, the infections in all the species reported in this paper occur in epidermal cells. The forms and structures of the galls are characteristic of the species causing them. The galls of most species are colored,

mostly light green or pale yellow, but a few have very bright colors. These colors are in the liquid contents of the surrounding uninfected host cells.

Galls are simple (*i.e.* single) or compound (*i.e.* aggregated into groups). The compound galls may result from over-crowding or from the infection of the epidermal cells of an older gall. Although the simple galls have definite forms, they may be modified as a result of being located on different organs of the plant, or to over-crowding or possibly to other causes.

These studies start with the early infections of epidermal cells of the host plant. Very little attention has been given to sexuality of the fungi or methods of infection. The infections of the host plants by all the species reported in this paper occur in epidermal cells which are not fully mature. Most species infect cells of more or less the same age but there are some exceptions. In some cases host cells of different ages in the same leaf are infected. Host cells are sometimes infected by two or more fungi of the same species; fungi in these multiple infections are usually the same age but there are some exceptions.

The contents of the infected host cell in most species studied is much more abundant and much denser than that of the surrounding cells but undergoes pronounced changes very rapidly. It may have a vacuolate, foamy appearance at first, gradually becoming dense, disintegrates and almost disappears in some species but persists in others. It may completely fill the space between the wall of the fungus and the wall of the host cell or it may divide into two layers, one clinging to the fungus to form the third or outer layer around the fungus, while the other part clings to the wall of the host cell. In some species the fungus wall is hard and brittle and breaks easily. In some species the disintegrating contents of the infected cell is granular and gives the wall around the fungus a warty appearance. The nucleus of the infected host cell stains deeply, enlarges at first, usually clings to the fungus but finally disappears when the fungus is about one-half full size. In some species it is very difficult to demonstrate its presence.

The fungus, in some species reported in this paper, enlarges very rapidly and completely fills the host cell while in other species it enlarges much more slowly and never completely fills the host cell.

In some species the host cell is filled very early in its development and then grows much faster than the fungus, so that in later stages it is not filled by the fungus.

The fungus is a uninucleate thallus and is usually called a prosorus previous to segmentation. The nucleus and nucleolus are exceptionally large at first, but lose their identity as the fungus approaches maturity. Two or more fungi are found frequently in a single host cell; they may be the same or different ages as shown by their development. These multiple infections are much more frequent in some species than in others. Two nuclei may occur in a single fungus but the writer is uncertain whether this is the result of division or the union of two fungi in the cell; however, it appears to be the latter.

Although the characters of the fungi have been considered most important for classification of species of *Synchytrium*, the author believes that the structures of the galls are much more reliable. In this connection it should be remembered that the characters of the fungi in collections of any species of *Synchytrium* made at different times may vary. The measurements of the fungus and number of sporangia are variable and the colors vary with age. Some species of this genus, so far as known, attack a single species of host plants, while others attack several species. Cross inoculations give the only positive evidence of inter-host relationships but this has been used in the study of very few species.

The descriptions in this paper are based on thousands of sections made from freshly collected material. No effort has been made to illustrate the entire life history of any species but all species reported in this paper have been studied by the author.

SYNCHYTRIUM ERIGERONTIS Cook on *Erigeron philadelphicus* L. (FIG. 1, A–D).

This species causes the infected cells to enlarge and almost fills them at all stages of its growth (A–C). The disintegrating contents of the host cell is prominent but the nucleus is inconspicuous. Multiple infections are common but rarely more than two fungi in a cell (D). When two are present, they are usually hemispherical. The wall around the fungus forms early, is thick and appears to be made up of three layers; the inner layer is thin, the middle layer

thick, and the outer layer composed of the disintegrating material of the host cell.

In cases of severe infections the leaves are thickened The infected cells enlarge and in some instances may extend from one to

FIG 1.

the other epidermal layer with very slight or no projections on the surfaces of the leaves and with very little or no modifications of the host tissues other than the epidermal cells in contact with the infected cell (C). In other cases the infected cell may extend only

part way through the leaf, the outer portion being covered with a layer of host cells so as to form a very simple, inconspicuous gall. Galls are more pronounced when over veins than in other places. The opening to the infected cell is small but always visible in properly cut sections. The host cells in contact with the infected cells are modified very slightly.

SYNCHYTRIUM GLOBOSUM Schröter on *Veronica perigrina* L. (FIG. 1, E, F).

In this species the fungus grows rapidly. More than one fungus in a host cell is rare. The wall around the fungus forms early, is thick at first but becomes thin with age (E, F) and is composed of three layers. The disintegrating contents of the infected host cell is usually conspicuous, especially in the outer part of the infected cell (E), but disappears almost completely (E, F) with age. In sections examined the nucleus of the infected host cell was rarely seen.

The infected cell becomes conical with the fungus in the basal part (E). The outer part of the infected cell is tubular and filled with the degenerating contents (E). The gall is conical and is composed of a few large, thin-walled cells (E). The basal parts of the leaf galls are embedded in the host tissues; the basal parts of the stem galls are embedded in the cortex but not as deep as the leaf galls.

SYNCHYTRIUM LYTHRI Cook on *Lythrum alatum* Pursh. (FIG. 2, A–E).

The fungus rarely fills the infected cell (A–D) except when very young but may do so in some cases. The disintegrating contents of the host cell may be inconspicuous or prominent. The wall around the fungus forms early, is usually thin and appears to be composed of three layers. The outer layer may be inconspicuous or rather prominent in some cases. The host cell nucleus may or may not be prominent (E).

The infected leaves usually become thickened (A), the infected cells become conical or pear-shaped and are embedded in the thickened host tissues (C, D). The host tissues grow to such an ex-

FIG 2

tent that the infected cells are deeply embedded (D) but the line where the cells have united over an infected cell can be traced in galls that have been cut properly (D) A very definite sheath is formed around the infected cell (C, D).

SYNCHYTRIUM FULGENS Schröter on *Oenothera laciniata* Hill (FIG. 3, A–D).

This species attacks plants of different ages in the same leaf. The fungus almost completely fills the enlarged host cell very soon after infection (A, B). Large and small fungi are frequently found in adjoining host cells indicating that infections of these cells have not occurred at the same time. Multiple infections are frequent. The disintegrating contents of the host cells are not abundant. The host cell nuclei are inconspicuous and rarely seen. The wall around the fungus forms early and may be very thin or very thick but becomes thin with age. In the material studied by the writer the wall was thin and appeared to be single except in a few cases.

The mesophyll is stimulated to excessive growth which causes a thickening of the leaf (A). The epidermal cells around the infected cells grow so as to almost but never completely cover them (C). The infected cell is embedded in the tissues of the host except at point of infection. The host cells form a definite sheath around the infected cell (C).

SYNCHYTRIUM CHILTONII Cook on *Stellaria media* (L.) Cyrill. (FIGS. 3, E, F and FIGS. 4, A–D). .

This fungus attacks the very young growths, mostly while in the bud. The fungus rarely fills the host cell until near maturity. Multiple infections are numerous; six or more fungi are frequently found in the same host cell (3, F); in most cases these fungi are the same or very nearly the same age, but in some cases they appear to be of different ages, as indicated by their development. The fungus grows rapidly and is usually granular or foamy in appearance. Two nuclei are occasionally present in the same fungus (4, C). The wall around the fungus is usually thin and the writer was not able to determine the number of layers. The contents of the host cell is usually inconspicuous but the host cell nucleus may persist until the fungus is about one-half mature.

The host tissues around the infected cells grow rapidly and cause thickenings of the infected leaves (4, A). The cortex of infected stems becomes very much thickened (4, B). The infected cells develop into rather large globular or oblong sacs which are not

filled until the fungus approaches maturity (4, A). In the stems, these sacs are embedded in the thickened cortex (4, B) and are oblong and longer than those in the leaves (4, B, C). The opening

FIG. 3.

over the infected cell is never closed.. A sheath of host cells is formed around the infected cell (4, A, C) and the epidermal cells at the opening are modified (4, A).

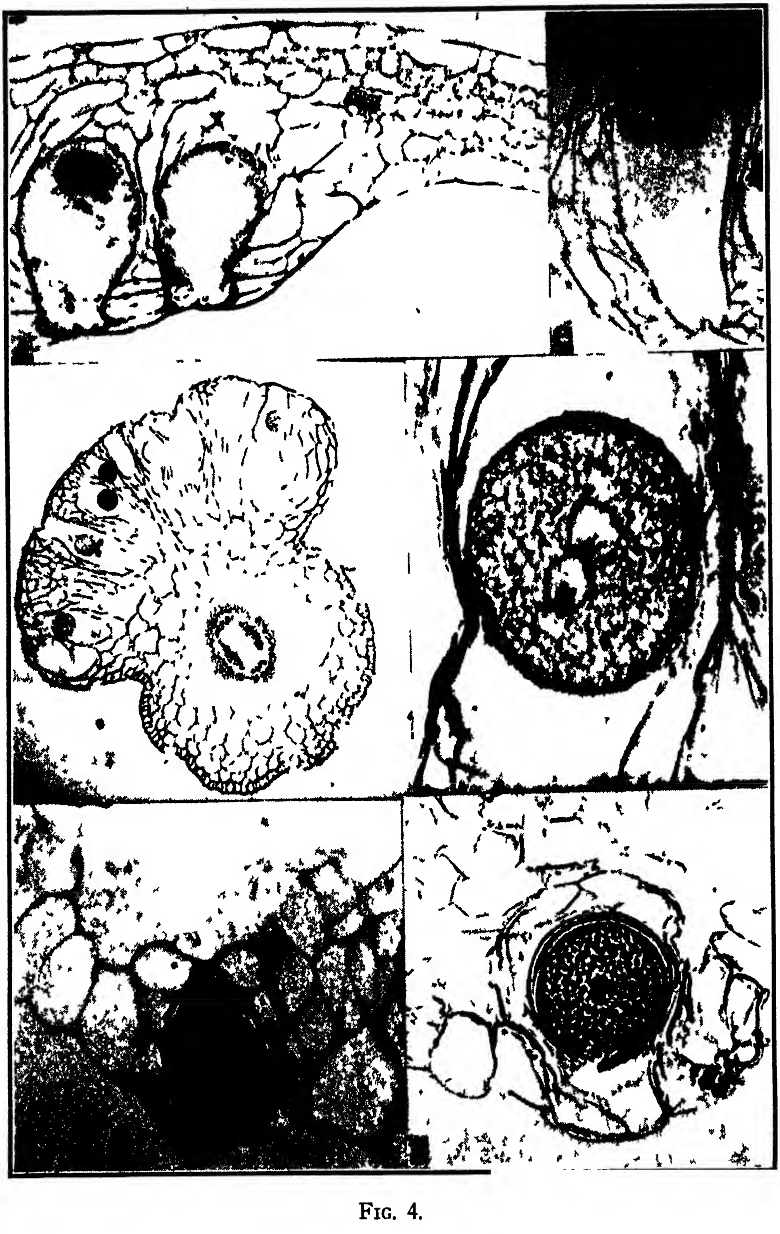

FIG. 4.

SYNCHYTRIUM CERASTII Cook on *Cerastium viscosum* L. (FIG. 4, E, F and FIG. 5, A–C).

The fungus grows so rapidly that a young, infected cell is soon filled (4, E, F) but in its later development the host cell grows more rapidly than the fungus and there is a large space between the fungus and the cell wall (5, A–C). Rarely one or more fungi are formed in a host cell but when two are present they are not necessarily the same age. The wall around the fungus is very thick when young (4, E, F) but becomes thin with age (5, A, C). It consists of three layers; the inner and middle layers are thin and usually so closely united as to appear as one. The disintegrating contents of the host cell are abundant at first, gradually decrease in amount (4, E, F). The host nucleus persists almost to time of segmentation of the fungus.

The galls are variable in size and, when abundant, they cause thickenings of the host tissues. The infected cell enlarges rapidly; the host tissues increase and almost surround it. When the infected cells are fully developed, they usually resemble the fully developed cells of *S. Chiltonii* (5, A) but are smaller and in some cases almost globular (5, B). The leaf thickens as a result of an increase in the amount of parenchyma and a sheath of one or two or three definite layers of cells is formed around the basal part of the infected host cell (5, A, B) which is embedded in the thickened host tissue. When the stems or petioles become thickened the infected cells are elongated and oval (5, C) and the surrounding cells very much modified to form sheaths around the infected cells.

SYNCHYTRIUM GERANII Clen. on *Geranium carolinianum* L. (FIG. 5, D–F and FIG. 6, A–C).

The fungus fills the infected cells soon after infection (5, D) but in a very short time these cells grow more rapidly than the fungus. The contents of the host cell is vacuolate at first but degenerates very rapidly. It is usually most abundant on the side next to the point of infection (5, F). It becomes granular as the fungus approaches maturity and is conspicuous (6, B). The host cell nucleus persists until very late, sometimes until the beginning of the segmentation of the fungus (6, A). The fungus appears to con-

sist of a foamy material (5, E) and contains an exceptionally large nucleus. It is surrounded by a wall consisting of three layers; the inner and middle layers are thicker than in most species and the inner is lighter in color; the outer layer consists of masses of dis-

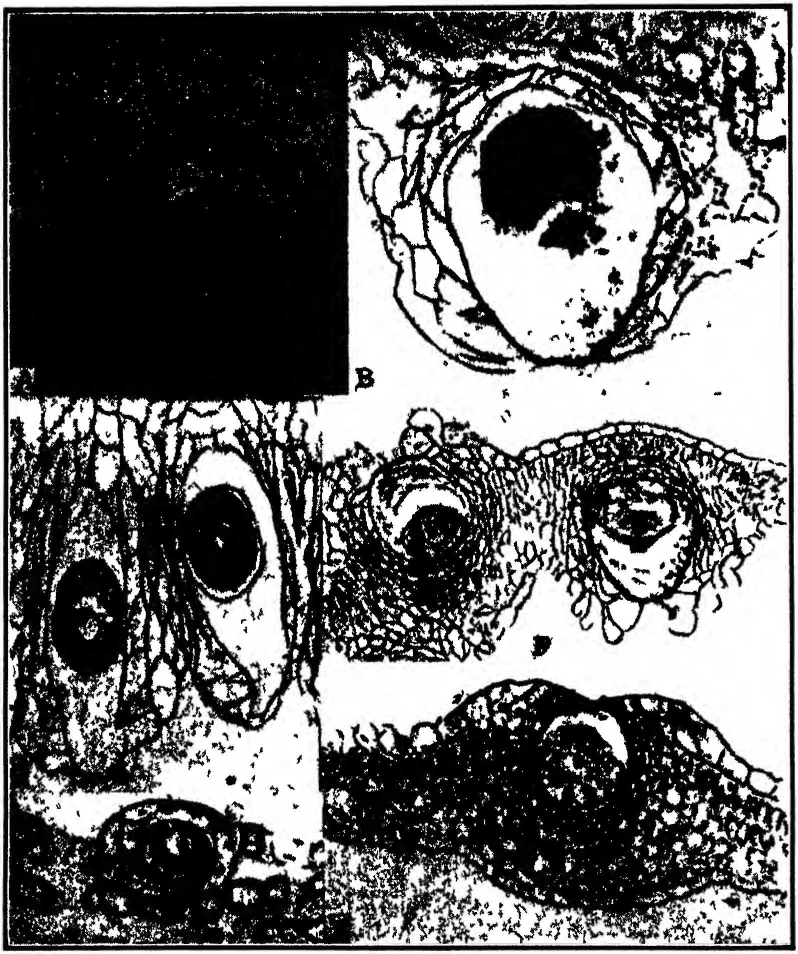

FIG. 5.

integrating contents of the host cell and is more conspicuous than in any other species reported in this paper (6, B). The inner and middle walls become very thin as the fungus approaches maturity (6, B).

FIG. 6.

The galls caused by this species are conspicuous by their bright red color. They are both simple and compound and cause pronounced deformities of leaves, petioles, and stems. The stems are sometimes swollen and fleshy like small tubers. The infected cells grow rapidly and the surrounding host cells are stimulated to cause

FIG 7

a thickening of the tissues The basal half of the leaf gall is surrounded by a sheath of modified host cells and the lower half embedded in the host tissues. The outer half is conical with a definite opening in the center which extends to the infected cell (5, F)

The cells around this opening are large and prominent. The infected cells in the fleshy growths are very long, with the fungus in the basal part, and are surrounded by an abundance of disintegrating material especially in the outer part (6, C).

SYNCHYTRIUM EDGERTONII Cook on *Dichondra repens* Forst. (FIG. 6, D, E and FIG. 7, A–E).

The infections of various ages sometimes occur in the same leaf (7, C). The fungus grows more slowly than the infected cell at first and large quantities of disintegrating host cell contents are usually present (6, E) but the amount decreases later (7, D, E). After a time the fungus grows rapidly and sometimes fills or nearly fills the host cell (7, C). The fungus is surrounded by a very thick wall (7, D) of three layers; the inner and middle are very hard and frequently break when struck by the microtome knife. The outer layer, composed of disintegrate contents of the host cell, is abundant at first but decreases with age. In most cases this wall is very thin at maturity.

The infected cell grows rapidly (6, D, E) and stimulates the surrounding host tissues. The epidermal cells grow rapidly and close over the infected cell very quickly (6, E). The host cells grow over the infected cell so that it becomes completely embedded but the point of infection can be traced in the sections that are cut properly (7, A). In some cases the infected cell lies about equal distance between the epidermal layers while in other cases it is nearer one than the other. When the fungus approaches maturity the surrounding host cells are very large. In some cases the mature gall is visible on only one and in other cases on both surfaces of the leaves (7, C). Compound galls are of common occurrence (7, C). When the fungus is mature the surrounding host tissues die and the fungus falls out (7, E). The stem and petiole galls are in the cortex tissue which finally breaks down.

SYNCHYTRIUM LEPIDII Cook on *Lepidium virginicum* L. (FIG. 8, A–F).

Soon after infection the fungus grows rapidly and completely fills the host cell and then grows more slowly. The mature fungus

is larger than in most species Multiple infections are common (A). The wall around the fungus consists of three layers (E); the inner one is very thin, the middle one slightly thicker, and the

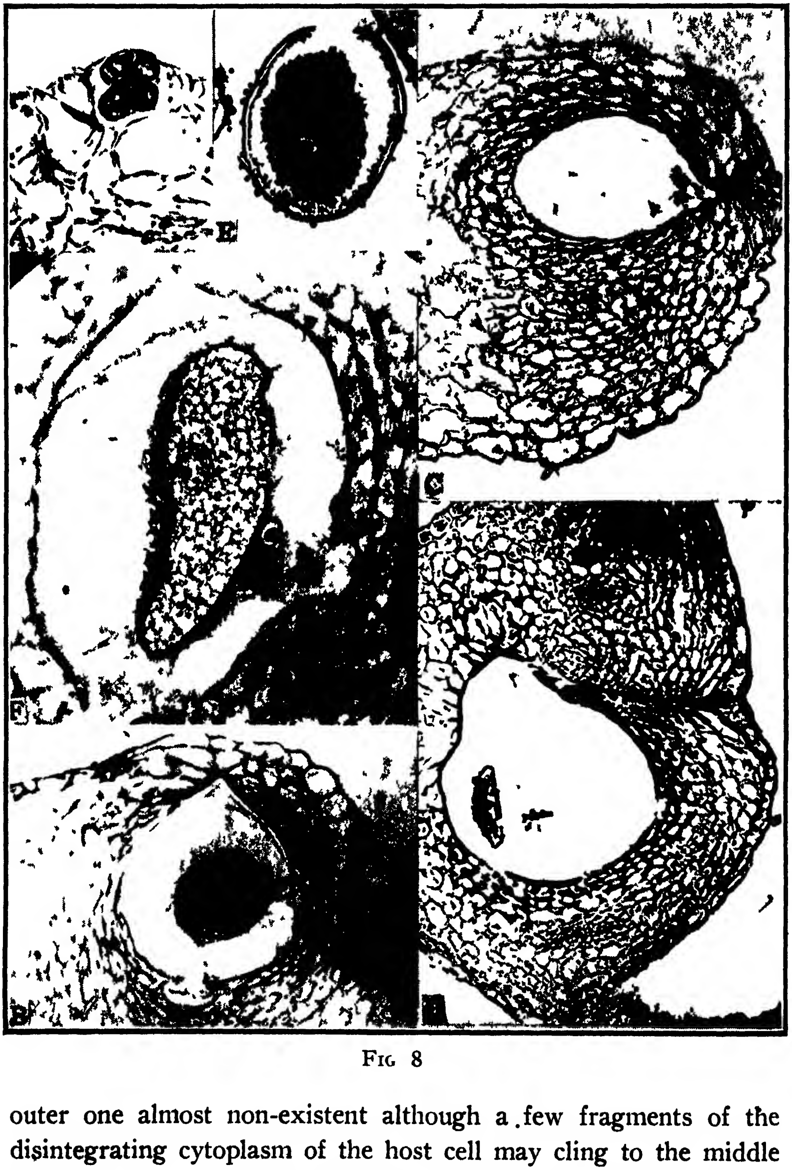

FIG 8

outer one almost non-existent although a few fragments of the disintegrating cytoplasm of the host cell may cling to the middle layer (E, F). In some cases it is almost impossible to distin-

guish between the inner and middle layers. In advanced stages the fungus does not fill the host cell (F).

The infected cells grow rapidly and the surrounding host cells are stimulated to excessive growths which cause galls that may be visible on either or both surfaces of the leaves and very conspicuous on petioles and stems. The growth around the point of infection is so great that the infected cell is completely embedded in the host tissues (B). The galls vary in form, are composed of a compact mesophyll of small cells; the cells next to the infected cells being the smallest (C, D). Compound galls are quite numerous. A very definite sheath is formed around the infected cell (B, D, F).

SYNCHYTRIUM AUREUM Schroeter on *Lactuca* sp. (FIG. 9, A–D).

This species attacks the epidermal cells on the lower surface of the leaves, rarely on the upper. The fungus grows rapidly and completely fills the host cell in its early development but in its later stages the infected host cell is slightly larger than the fungus (B, C). The wall around the fungus is thin and shows two distinct layers. The disintegrating contents of the infected cell is sparse. The nuclei of the infected cells are rarely seen.

The infections are almost entirely restricted to the lower surface of the leaf. The infection is followed by the formation of a dome-shaped structure with the concave side on the lower surface of the leaf (D). The galls are formed on the under surface regardless of whether the infection occurs in the lower or upper epidermis. In some cases the mesophyll cells just above the infected cell become elongated (A) while in other cases they are only slightly affected (B–D). However, the host tissues are modified more or less throughout the entire dome and in the palisade layer the cells are reduced to more or less cubical form.

SYNCHYTRIUM HYDROCOTYLES Cook on *Hydrocotyl umbellata* L. and *H. Canbyi* Coult. & Rose (FIG. 9, E, F and FIG. 10, A–C).

The fungus usually fills the infected cell until it is mature (10, A–C). Two fungi are occasionally observed in the same cell. The wall around the fungus is usually thin and it is difficult to de-

termine the number of layers. The disintegrating contents of the host cell is abundant but gradually decreases with age. The host cell nucleus is not prominent

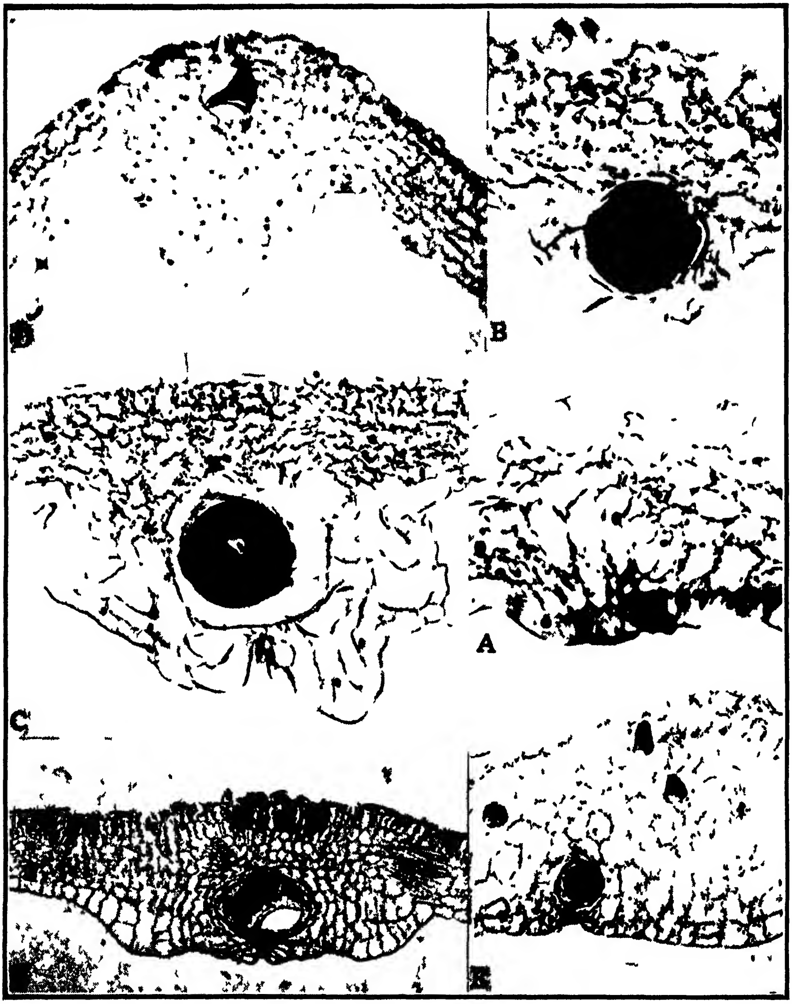

FIG. 9.

The infected cell grows rapidly and the surrounding tissues are stimulated to excessive growth and the formation of a dome with the concave side usually on the under surface of the leaf. However, when the infected cell is on the upper surface the concave

side is also on the upper side of the leaf. These concave structures are not formed on the margins of the leaves or petioles. The epidermal cells around the infected cell grow so that the opening is

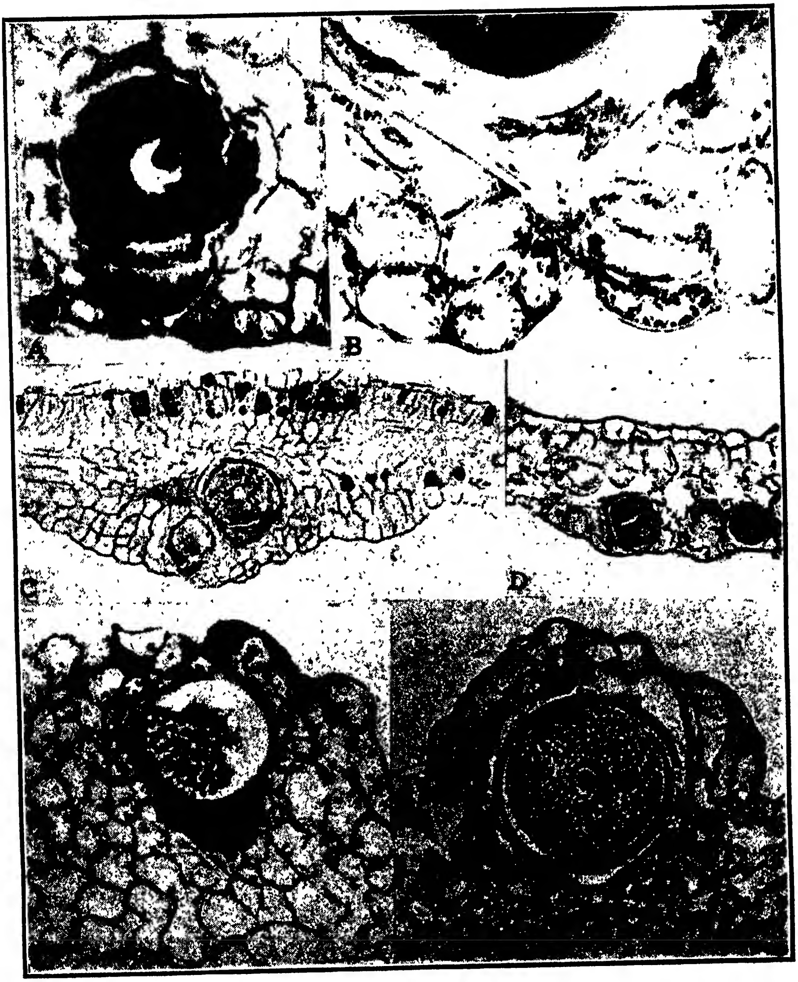

FIG. 10.

nearly or completely closed (10, B, C) but the openings can be traced if the sections are cut properly. Two fungi are sometimes found in the same gall, but one is usually older than the other. The mesophyll in the galls is composed of small compact cells.

SYNCHYTRIUM STACHYDIS Cook on *Stachys agraria* Cham & Schlect (FIG 10, D–F and FIG 11, A–C)

The fungus almost completely fills the infected cell and is about one-third full size before the start of gall formation The wall around the fungus is thick until the fungus is about two-thirds full

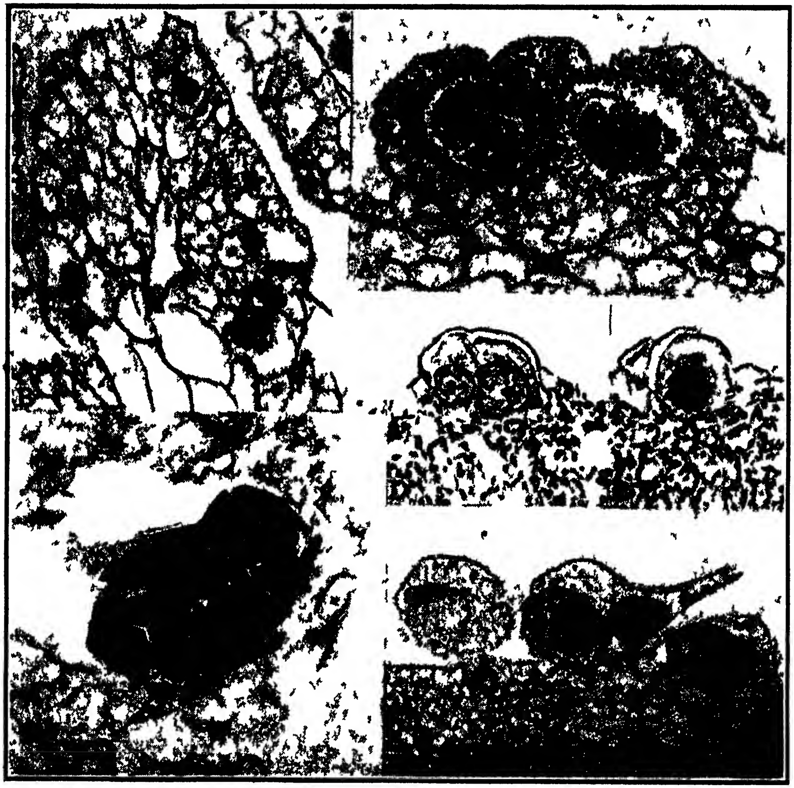

FIG 11

size (F) After that it becomes thin It appears to be composed of three layers, the inner is thin, the middle thick (F) and the outer which is composed of degenerate contents of the host cell is abundant at first but decreases with age (E, F) The nucleus of the host cell persists until the fungus is about one-half full size

Both the infected and the surrounding host cells grow rapidly The epidermal and other host cells surrounding the infected cell

FIG 12.

grow over and form a gall made up of large thin-walled cells with infected cell submerged at some distance from the surface. Many epidermal cells of this gall become infected and result in the formation of large compound galls (B).

The host plant is attacked by mites which cause galls that are frequently mixed with the galls caused by the *Synchytrium* but

can be distinguished in micropreparations by the different structures and frequently by the presence of the mites, especially in young mite galls.

SYNCHYTRIUM MODIOLIENSIS Cook on *Modiola caroliniana* (L.) G. Don. (FIG. 11, D–F and FIG. 12, A–D).

The fungus grows rapidly and fills or nearly fills the infected cell which also grows very rapidly (D, E). Two or three fungi in a single host cell is quite frequent. The only case of infection of a trichome was found in this species (F). The wall around the fungus consists of at least two very thin layers which are so closely united as to appear as one. The disintegrating contents of the infected cell is abundant and foamy in appearance at first but decreases very rapidly and practically disappears at maturity, so that there is little or no third layer in the wall around the fungus.

The galls are spherical unless crowded and rest on the surface of the host (A, B). There is very little modification of the host tissues. The epidermal cells on three sides of the infected cells grow so as to form a covering of about two layers, or sometimes three layers at the base, over the infected cell (A). The epidermal cells on the fourth side start to grow a little later and finally meet the growths from the other sides. The result is a small opening where the growths from the four sides come together that is a little to one side of the center (A). When a gall is cut properly this is very evident but when cut at right angles it is not visible (B). Galls on the stems may be irregular in form or undeveloped (C).

Imperfect galls.

In some cases the fungi die and the resulting galls are imperfect, the development depending on the period of infection before the death of the fungus (FIG. 12, E and F). This may occur in any species.

SUMMARY

The infections in the species reported in this paper always take place in epidermal cells of the host plant before they are fully mature and are more numerous on leaves than on other organs.

Some species appear to be able to attack epidermal cells that are more mature than other species.

In most cases the epidermal cells are infected by a single zoöspore but multiple infections have been found in every species and are quite common in some species, *S. Chiltonii* on *Stellaria media* and *S. Lepidii* on *Lepidium virginicum*, although less common on the latter. The fungi within the cells are usually of about the same age as indicated by development, but there are some exceptions, especially in the case of *S. Chiltonii*.

Both the infected host cells and the fungi continue to grow until the fungi are ready for segmentation. The fungus has a foamy appearance but finally becomes filled with spherical bodies which are probably oil globules. The nucleus is very large and clear, except for the presence of the nucleolus and dark staining materials.

The infections in a leaf area are usually very nearly the same age but there are some exceptions; *e.g.*, *Synchytrium fulgens* on *Oenothera laciniata* and *Synchytrium Stachydis* on *Stachys agraria*.

The fungi enlarge until the host cells are practically filled. After that the infected cell in most species usually grows faster than the fungi.

All species studied cause the formation of galls but these abnormal structures caused by some species are much more conspicuous than those caused by other species (*e.g.*, *Synchytrium Geranii*).

The epidermal cells immediately around the infected cell are excited to growth and in all cases except in that *S. fulgens* grow and divide in such manner as to form galls. The cells in contact with the infected cell are modified and form definite sheath structures around the infected cells. Some species cause very little or no modifications of host tissues (*e.g.*, *S. modioliensis* and *S. Erigerontis*). Some species cause the infected leaves to thicken; the infected cells are embedded in these thickened leaves with very little or no gall formation. Some species cause the formation of galls on the surfaces of leaves and little or no modifications of the leaves (*e.g.*, *S. modioliensis*).

The galls start with the growth of epidermal cells in contact with the infected cells but the cells of other tissues may be in-

volved later. In some cases one-half of the infected cell is submerged, while in other cases it may be completely submerged. This is due to the growth of the host tissues. In cases where the infected cell is completely submerged there may be no gall or only a thickening of the leaf (*e.g., S. Edgertonii, S. Erigerontis,* and *S. fulgens*).

The galls caused by different species of *Synchytrium,* for the most part, are distinctive and much more important for descriptions and determination than the characters of fungi that cause them.

Galls may be modified by overcrowding. Compound galls usually result from infections of epidermal cells of older galls.

The mature fungus of all species studied is embedded in the tissues of the host, except in the case of *S. modioliensis* in which the fungus exerts very little influence on the structure of the leaf. This gall rests on the surface of the leaf or other organ.

The infections on the petioles and stems cause growths of the cortex which usually result in malformations which are very pronounced in some species.

In some species there is a definite opening to the infected cell until maturity of the fungus, while in other species the infected cell is completely enclosed in the gall which is formed from the surrounding host cells. However, a definite line between the host cells that have closed over the infected cells can be traced if the sections are cut properly.

The author wishes to express his thanks to Dr. C. W. Edgerton and others who have assisted in and given encouragement to this work. They have been mentioned in the preceding paper. Dr. Edgerton made all the photographs.

DEPARTMENT OF BOTANY,
LOUISIANA STATE UNIVERSITY,
BATON ROUGE, LOUISIANA

EXPLANATION OF FIGURES

FIG. 1. A–D, *Synchytrium Erigerontis* Cook. A, Early infections in lower epidermis (× 224). B, Advanced stage, not exactly through the center; note wall around fungus and small amount of disintegrating contents of host cell (× 392). C, Infection in upper surface of leaf; note that the infected cell extends from epidermis to epidermis, and that it is not completely

covered by the upper epidermis (× 192). D, Two hemispherical fungi in a single host cell (× 192). E, F, *S. globosum* Schroeter; E, Gall and infected cell; note large cells of gall and disintegrating contents of infected cell (× 192). F, Same showing many small sporangia (× 192).

FIG. 2. A–E, *S. Lythri* Cook. A, Showing thickened leaf of host plant and early infections; the infected cells near the upper surface that appear to be submerged have not been cut through the center (× 96). B, Early infection in a stem. C, Shape of infected leaf cell surrounded by sheath formed from host cell tissue (× 224). D, A much later stage with lower magnification; note long tube and modified cells at surface (× 144). E, Showing fungus with thin wall and disintegrating host cell nucleus (× 384).

FIG. 3. A–D, *S. fulgens* Schroeter. A, Showing thickened leaf of host and infections of different ages on both surfaces of leaf (× 192). B, Showing early infections on lower surface of leaf. C, Showing growth of epidermal cells, partially covering infected cell and sheath of host cell tissue around infected cell (× 192). D, Showing large number of small sporangia and that the epidermal cells have not completely covered the infected cell (× 192). E–F, *S. Chiltonii* Cook. E, Showing a single infected cell on lower surface of leaf (× 312). F, Showing single and multiple infected cells on upper surface of leaf (× 192).

FIG. 4. A–D, *S. Chiltonii* Cook. A, Showing two large infected cells in lower surface of leaf surrounded by modified host cells; part of leaf to the right is not modified (× 66). B, Showing thickened cortex on one side of stem (× 16). C, Showing infected cell of infected stem with two fungi and modified host tissue (× 80). D, Showing a large fungus with two nuclei (× 280). E, F, *S. Cerastii* Cook. E, Showing early infection on under surface of leaf (× 328). F, Showing a later stage (× 280).

FIG. 5. A–C, *S. Cerastii*. A, Showing the shape of the infected cell in advanced stage and the sheath of host tissue around it (× 134). B, Showing slightly different form of infected cell and sheath of host tissue (× 160). C, Showing infected cells with surrounding sheath of host tissue in stems (× 140). D–F, *S. Geranii* Clen. D, Showing early infection in lower surface of leaf (× 280). E, Showing early development of gall in upper surface of leaf and that the epidermal cells have not closed over the infected cell (× 160). F, Showing advanced development of galls on both surfaces of leaf; note sheath of host tissue around infected cells, that the infected cells are not covered by the epidermal cells and the large epidermal cells around the opening (× 66).

FIG. 6. A–C, *S. Geranii*. A, Showing fungus and host cell nucleus (× 312). B, Showing stage in formation of sporangia and disintegrating content of host cell (× 312). C, Showing a single infected cell from fleshy stem; note shape, sheath of host tissue and disintegrating contents of host cell (× 50). D & E, *S. Edgertonii* Cook. D, Showing two infected cells in upper epidermis of leaf (× 312). E, Showing more advanced infection in upper epidermis of leaf and growth of epidermal cells over infected cells and disintegrating contents of host cells (× 312).

FIG. 7. A–E, *S. Edgertonii* Cook. A, Showing the complete closing of the host cells over the infected cell but that the line of union can be traced (× 624). B, Showing a gall that originated from a cell in upper epidermis

and the modified host cells around the infected cell (× 96). C, Showing compound gall and infections of different ages (× 66). D, Showing an advanced stage in development of sporangia (× 312). E, A mature gall in which the host tissues are disintegrating (× 96).

FIG. 8. A–E, *S. Lepidii* Cook. A, Showing early multiple infection on lower surface of leaf (× 280). B, Advanced stage showing young gall and the closing of the host tissues over the infected cell (× 80). C & D, Showing two galls composed of compact, small mesophyll cells and the opening to the infected cells (× 80 and × 66). E, Showing fungus with two nuclei, the wall around the fungus and the small amount of disintegrating contents of the host cell (× 280). F, Showing a fungus and nucleus of the host cell; note the notch in the surrounding host cell tissue (× 200).

FIG. 9. A–D, *S. aureum* Schroeter. A, Showing early infection in cell of lower epidermis and modifying host cells of the mesophyll (× 160). B, More advanced stage in which the mesophyll is not modified but surrounding epidermal cells are enlarged (× 160). C, More advanced stage showing the enlarged cells of the gall (× 134). D, Showing infection in the upper epidermis and an advanced stage in the formation of the gall on the under surface; also showing the dome over the gall (× 80). E & F, *S. Hydrocotyles* Cook. E, Showing an early infection on the under surface of the thickened leaf (× 66). F, A later stage showing the closing of the host tissues over the infected cell and the disintegrating contents of the infected host cell (× 66).

FIG. 10. A–C, *S. Hydrocotyles* Cook. A, Later stage showing growth of infected cells over infected cell (× 280). B, Showing closing of the host cell tissues over the fungus at point of infection (× 280). C, Showing two fungi of different ages in the same gall (× 66). D–F, *S. Stachydis* Cook. D, Showing infection of leaf (× 120). E & F, Showing later infections, wall around the fungi and degenerate contents of host cell (× 328).

FIG. 11. A–C, *S. Stachydis* Cook. A, Showing two galls in early stages of development (× 160). B, Showing infections in epidermal cells and also one cell with three sori. C, Showing sporangia (× 328). D–F, *S. modioliensis* Cook. D, Showing early infection of two epidermal cells in upper epidermis (× 312). E, Showing an infected cell and first growth of an epidermal cell (× 312). F, Showing infection of an epidermal cell (× 160).

FIG. 12. A–D, *S. modioliensis* Cook. A, Showing almost complete gall in which the epidermal cells are meeting to one side of center (× 280). B, Showing two galls; the one on the right shows the opening to the infected cell; the one on the left is cut at right angles to the first and the opening is not shown (× 280). C, Showing crowded galls on stem (× 160). D, Showing sporangia (× 66). E, *S. Geranii*, showing imperfect gall following death of fungus (× 80). F, *S. Lepidii*, showing imperfect gall following death of fungus (× 160).

A COMPARATIVE STUDY OF TWO CLOSELY RELATED ROOT-ROT FUNGI, CLITOCYBE TABESCENS AND ARMILLARIA MELLEA

Arthur S. Rhoads [1]

(with 5 figures)

INTRODUCTION

The root rots produced by these two closely related mushroom or toadstool fungi are so much alike in general aspect that, in the absence of sporophores or the isolation of the fungus, they may be confused readily. The correctness of the diagnosis of these root rots made under such circumstances, particularly in sections where both possibly occur, may be questionable in some cases.

Considerable confusion also has existed for many years in the literature with respect to the identity of *C. tabescens* Scop. ex Bres., despite Bresadola (**3**) having shown in 1900 that the united *Clitocybe* best known in the United States as *C. monadelpha* (Morg.) Sacc. is identical with the European plant described as *Agaricus tabescens* by Scopoli in 1772. Even more than two decades after the publication of Bresadola's work, with many mycologists accepting the identity of the fungus in its true light, we find Rea (**10**), Buller (**5**, p. 91), and certain others regarding it merely as an exannulate form of *A. mellea* Vahl ex Fr. The writer in 1925 (**12**) published the taxonomy of *C. tabescens*.

The following, subsequently published remarks by Kauffman (**7**, pp. 206–207), who accepted Bresadola's consideration of the American plant in question as synonymous with *C. tabescens* of Europe, are of interest in this connection:

[1] Formerly Plant Pathologist of the Florida Agricultural Experiment Station, in charge of the Citrus Field Laboratory at Cocoa, where the work here reported was done. Acknowledgment is made to the Division of Forest Pathology of the U. S. Department of Agriculture for their interest and support, which have made it possible to prepare the results for publication.

"Under this name Morgan's American species, *C. monadelpha,* has finally come to rest—let us hope—in peace. There are still amateurish workers, who get a reaction out of suspecting that *C. tabescens* may after all be only a form of *Armillaria mellea,* and perchance a few who try to blow the breath of life into the long buried corpse of *Clitocybe parasitica* Wilcox, in order to show that it was either *C. tabescens* or *Armillaria mellea* or a genuine species." Under the heading of "Synonymous and excluded or doubtful species" he remarked: "*C. parasitica* Wilcox was never understood by mycologists, and should be deleted from the literature."

How delightfully simplified mycology could be rendered by the simple expedient of relegating to a state of innocuous desuetude those species that are not understood. It is obvious from a consideration of Wilcox's description and illustrations (**20**) that there can be no question in regard to the identity of the Oklahoma root-rot fungus which he described as *C. parasitica.* But it was unfortunate that he considered it a distinct species from the one that had been so well described from Ohio by Morgan (**9**) as *Agaricus* (*Clitocybe*) *monadelphus,* basing his distinction simply on slight differences in morphology and the parasitic habit of growth. As the writer (**12**) has pointed out previously, Wilcox's assertion that the Oklahoma fungus "is always parasitic in habit" is contradicted subsequently by his own statements, and the slight morphological differences claimed by him are of little value. American mycologists, with the exception of Kauffman, appear to have been in general agreement that the species described by Wilcox is synonymous with Morgan's *Agaricus monadelphus.* It has long been recognized that this fungus occurs both parasitically and saprophytically, not only in Oklahoma but also in the adjoining States of Arkansas and Missouri and a number of others, chiefly southern ones.

Another point in Wilcox's paper (**20**) subject to criticism is his mention and illustration of black, stringlike, rhizomorphic strands, both cortical and subterranean, similar to those commonly associated with *A. mellea,* as a characteristic feature of the *Clitocybe* root-rot fungus in Oklahoma. Despite extensive field studies of the disease caused by this fungus in Florida over a period of 18 years, the writer has never observed the occurrence of such struc-

tures in connection with it,[2] though they have been observed in connection with the root rot caused by the closely related fungus, *A. mellea.* Wilcox (20) stated that subterranean rhizomorphs grew out into the soil for considerable distances from attacked trees, citing 8 feet in one case and 10 feet in another. Although he stated that, so far as he was aware, *A. mellea* did not occur in Oklahoma, a careful study of his bulletin, together with the fact that both this fungus and *C. tabescens* have been reported (1, p. 48) as "commonly parasitizing a number of plants, including privet hedges, apple and peach trees, as well as grape vines" in Arkansas, has forced the writer to conclude long ago that both fungi occur in Oklahoma and that the similar root rots caused by them must have been confused by Wilcox in the absence of cultural studies. This conjecture is further supported by the fact that Wilcox (20, p. 19) mentioned that he had detected the phenomenon of phosphorescence in the subterranean rhizomorphic strands. A recently published host index to plant diseases in Oklahoma (4) lists both root-rot diseases. *A. mellea* is listed as occurring on apple, blackberry, cherry, elm, maple, plum, privet, rose and sycamore, while *C. tabescens* is listed as occurring on apple, cherry, grape, peach and plum.

The close relationship between *C. tabescens* and *A. mellea* as observed by Totten (19) and Richards (18) in preliminary cultural studies, as well as in the investigations of the writer (12) in Missouri, and subsequently in Florida (13) over a period several years, have prompted him to make a comparative study of these fungi. While it was necessary to abandon this work before it was carried to the point desired, the results thus far secured have revealed striking and consistent differences that should definitely refute the view expressed by a number of mycological workers that *C. tabescens* is merely a form of *A. mellea.*

SOME DISTINGUISHING CHARACTERS OF THE ROOT ROTS

Despite the great similarity of *C. tabescens* and *A. mellea* with respect to their mode of attack and the symptoms exhibited by attacked plants, their ability to develop either parasitically or sapro-

[2] The rhizomorph indicated by him on the grapevine rootstock in Missouri (12, pl. 2) is now considered questionable.

phytically, and their marked predilection for oak roots, there are a number of features in which these root rots, as well as the fungi producing them, differ.

While both fungi commonly develop whitish- or chamois-colored rhizomorphic strands and sheets between the bark and the wood of attacked roots of woody plants, and also in pure cultures, according

FIG. 1. Cultures of *C. tabescens* 10 days after inoculation with isolate from poinsettia, showing extensive development of rhizomorphs in comparison with scant growth of mycelium

to the writer's observations the black, rounded or flattened, cortical and hypogeal, stringlike rhizomorphs so commonly produced by *A. mellea* are not produced by *C. tabescens*. But, both fungi may develop blackish, indurated, xylostroma outgrowths extruded through longitudinal fissures in the bark of attacked roots.

The peculiar perforate character of the mycelial sheets of *C. tabescens* pointed out by the writer (**16**) and described in detail (**17**), though not always well developed, is a characteristic feature of the root rot caused by that fungus, but appears to be lacking in

the case of the root rot caused by *A. mellea.* Moreover, the mycelial sheets in the case of *C. tabescens* appear to have a less pronounced fan-shaped type of marginal development than in *A. mellea.* Further differences between these closely related root-rot fungi in pure cultures are pointed out in the following section.

COMPARATIVE GROWTH AND FRUITING OF THE FUNGI IN PURE CULTURES

A few investigators have grown *C. tabescens* in pure cultures and, where cultures of *A. mellea* were available, the close resemblance of these two fungi has prompted comparisons. The basis for these comparisons heretofore has been limited to a few isolates. In 1917, Totten (**19**) reported growing both fungi in pure cultures on several media and showed that, while closely related, they are distinct. In 1921, Siggers [3] prepared a progress report of his comparison of *C. tabescens* isolated from a specimen of eucalyptus root sent from Florida and *A. mellea* isolated from a rhizomorph attached to the root of a white ash at Madison, Wis. In 1923, Richards (**18**), who continued this work after Siggers left for Central America, briefly reported on cultural studies of these fungi, comparing the isolate of *C. tabescens* from Florida with 6 isolates of *A. mellea* from various sources. The close similarity in appearance of cultures of these fungi was pointed out, and slight differences in *A. mellea* from different hosts were shown. She reported that *C. tabescens* produced sporophores but that all efforts to obtain them from *A. mellea* failed. In 1925, the writer (**12**) reported the results of cultural studies of *C. tabescens,* comparing his isolate of this fungus from grapevine in Missouri with the isolate from eucalyptus from Florida, which grew with greater luxuriance.

During the course of his investigations in Florida the writer has studied isolates of *C. tabescens* from a great array of host plants from this State and a number from trees in other States, including 5 from Alabama, 2 from Louisiana and 1 each from the District of Columbia and Virginia. The isolates of *A. mellea* that have been studied comprise 4 from Canada, 3 from California, 1 from Wisconsin, 2 from Pennsylvania, 2 from Florida, and 6 from Euro-

[3] Siggers, Paul V. Summary of comparative study between forms of *Armillaria mellea* and *Clitocybe monadelpha.* Typewritten report. 1921.

pean and other countries, the latter consisting of isolations by Cool, Gregor-Wilson, Rant, Reitsma (2), and the Centraal-Bureau voor Schimmelcultures. In addition, the tropical analogue of this fungus, *A. fuscipes* Patch, was represented by isolates from *Albizzia*

FIG. 2. Bottom of flask culture of *C. tabescens* from horsetail beefwood (*Casuarina equsetifolia* L.), showing radiating wrinkles in broad, thalluslike rhizomorphs and average growth of 2.5 cm. in 24 hour period following outlining of margins. Natural size.

lophantha Benth. and *Camellia sinensis* (L.) Kuntze made by Gadd.

The rapidity of mycelial growth and rhizomorph formation in *C. tabescens* have shown considerable variation in the different isolates, being fairly rapid in some and quite slow in others. Some

isolates of the fungus have developed a luxuriant growth of rhizomorphs starting within 3 days to a week. In many cases the development of rhizomorphs started and made considerable headway before there was any appreciable growth of mycelium on the surface of the agar. In other cases, however, the development of the rhizomorphs was less rapid and occurred only after the development of more or less mycelial growth on the surface of the agar. In some cases little or no development of rhizomorphs occurred. These differences were not necessarily confined to certain isolates of the fungus from particular plants. Even in a series of isolations from a particular plant or a series of transfers from a single isolate considerable variation occurred, with the result that some cultures grew rapidly and made a luxuriant development of rhizomorphs, while others grew slowly, with very scanty development of rhizomorphs. Transfers from old cultures in which the mycelial mat on the surface of the agar slant had developed a hard, brittle crust did not develop with the readiness of transfers from younger cultures. In some instances subcultures from cultures that developed rhizomorphs luxuriantly developed few or none. In most cases, however, it was found that rhizomorph development could be greatly stimulated by transfer to a rich nutrient medium.

A. mellea behaved similarly and proved even slower and more temperamental in culture. Reitsma (11) found that the formation of rhizomorphs by this fungus was completely suppressed by constant subculturing in liquid media but that upon transference to a solid substratum rhizomorphs gradually developed again. Lisi (8), who studied 47 isolates of this fungus from a wide variety of habitats and localities, found many distinct varieties, a number of isolates studied from a restricted geographical area showing at least 6 distinct variants. He made a physiological study of a selected group of 10 morphologically distinct variants. Benton and Ehrlich (2) found a wide variation in the character of mycelial growth, rhizomorph production, and rate of growth in 10 isolates of *A. mellea* from a single suscept species (*Pinus monticola* Lamb.), though the replications from a single isolate were found to have similar cultural characteristics. They also found the tested isolates to vary in degree of saprogenicity and in response to differences in wood-moisture content, temperature, and pH values.

The writer has found that the nutrient medium exerts considerable influence on the character, rate, and luxuriance of growth of the mycelium and rhizomorphs in both *C. tabescens* and *A. mellea.* Cultures of these fungi on potato-dextrose agar usually developed slowly and tended to make a rather weak growth. The addition of maltose or malt extract or other sources of sugar greatly stimulated mycelial growth and rhizomorph production. It was found in the writer's earlier cultural work in Missouri (**12**) that *C. tabescens* grew well on prune and raisin agars. Most of his cultural work in Florida with both this fungus and *A. mellea* has been conducted on the standard potato-dextrose agar with the addition of 20 gms. of either maltose or malt extract per liter. In some cases a little cane sugar was added. The addition of peptone to such agar was not observed to stimulate greater luxuriance of growth. For flask cultures such plant material as oak sawdust, diced potatoes, carrots or bread, pieces of petioles of castor bean leaves, or cubes of oak wood or banana stems have been added to the agar. The addition of oak sawdust appeared to induce a more vigorous, whiter, and fluffier growth of mycelium. On the latter medium *C. tabescens* made a much more rapid growth than *A. mellea,* which Edgecombe (**6**) found to be an exceedingly slow grower on artificial media in comparison with 5 other wood-inhabiting fungi.

Both fungi are characterized by the common, but by no means invariable, tendency for the agar to develop a dark brown discoloration in advance of the mycelial growth. In isolations of these fungi from roots and in transfers of them from stock cultures a distinct browning of the agar in advance of the inoculum frequently developed before mycelial growth became visible to the unaided eye. This browning of the agar appeared to develop principally in the cases where the cultures ran chiefly to mycelium rather than to rhizomorphs. The discoloration of the agar increased with the growth of the fungi until in cultures a month old the upper half of the agar slant in test tubes may become discolored dark brown.

RHIZOMORPH PRODUCTION

The characteristic feature of both *C. tabescens* and *A. mellea* is the usual early development of whitish rhizomorphs growing downward into the agar from the inoculum. Even in cultures of *C.*

tabescens started from basidiospores, rhizomorphs invariably develop before there is much growth of mycelium. In fact both fungi frequently run more to the production of rhizomorphs than of mycelium, though the development of rhizomorphs varied according to the culture media and the vigor of the isolate.

In transfers of bits of mycelium from either roots or cultures a series of whitish rhizomorphs usually developed from the bottom of the inoculum simultaneously with or shortly after the beginning of mycelial growth on the surface of the agar in the case of both fungi. These rhizomorphs grow downward into the agar fairly rapidly as rounded or flattened, simple or branching, tortuous, antlerlike structures, the tips of which may be pointed, blunt, or flattened (FIG. 1). As these rhizomorphs became older numerous, short, threadlike, lateral branches often developed. In vigorously growing cultures the rhizomorphs commonly ramified through the agar in all directions. Occasionally one or more of them became greatly flattened and thalluslike in appearance, though this type of rhizomorph rarely developed in test tube cultures.

After growing down into the agar in test tube and flask cultures the ends of some of the rhizomorphs soon turned upwards of their own volition and developed until their tips pushed through the surface of the agar, after which there was little further elongation. In *C. tabescens* the tips remained characteristically blunt and rarely protruded more than 1/16 to 3/32 of an inch above the surface of the agar and remained light-colored, though darkening somewhat with age. In *A. mellea,* however, the tips often projected as much as 1/4, and occasionally 1/2, inch, turning dark reddish-brown to blackish following exposure to the air and became attenuated or needlelike. The development of these elongated, dark reddish-brown to blackish, needlelike, aerial rhizomorphs protruding above the surface of the agar varied somewhat in cultures from different sources and was most pronounced in *A. fuscipes.* The dissimilar character of the aerial rhizomorphs is one of the main distinguishing characters between *C. tabescens* and *A. mellea,* including its tropical analogue. Up to the point where the rhizomorphs protrude through the surface of the agar these two fungi appear to be inseparable on the basis of rhizomorph development since either may exhibit a considerable range of variation. The rhizomorphs

that develop down into the agar remain white for a time in both fungi but become chamois-colored with age.

The growth and development of the rhizomorphs are best studied in flask cultures, where they may be observed growing along the bottoms and up the sides. In both *C. tabescens* and *A. mellea* all

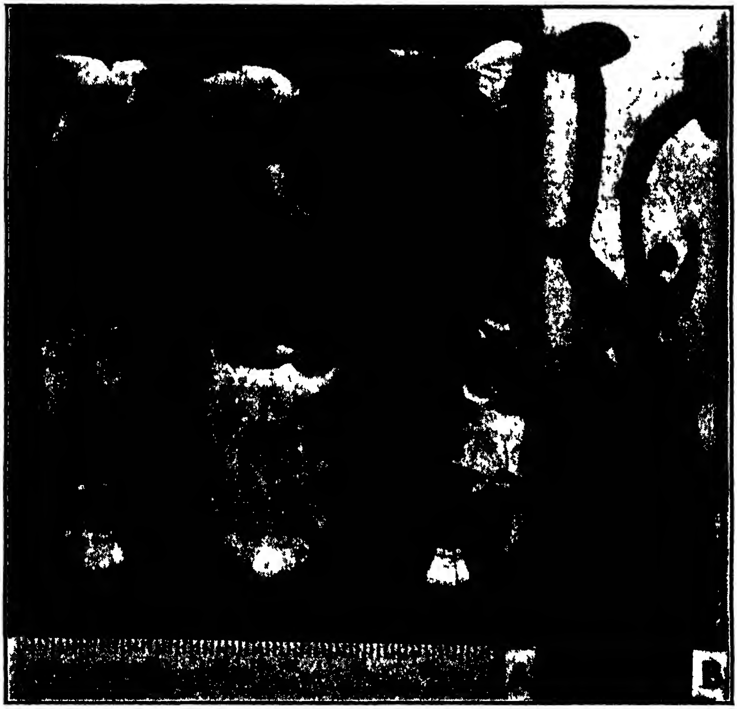

FIG. 3. A, Second production of sporophores in 6 week old cultures of *C. tabescens* from poinsettia, the tubes from left to right first developing mature ones in 28, 33 and 38 days, respectively B, cluster of mushrooms developed from end of rhizomorph at top of agar slant in 18 mm. test tube 31 days after isolation from painted copperleaf.

gradations of rhizomorph formation from simple or branching, threadlike ones to much-branched, greatly broadened, thalluslike structures as much as an inch wide at the ends (FIG. 2) may be found in an assortment of cultures from different isolates. The latter type of rhizomorphs, which occurred much more frequently than the former, is characterized by a series of radiating wrinkles.

After the fungi became well established the rhizomorphs often developed for a time with considerable rapidity. In order to secure some accurate measure of the rate of growth attained under favorable conditions, the marginal outlines of a number of broad, thalluslike rhizomorphs growing across the bottom of a 500 ml. Erlenmeyer flask culture of *C. tabescens* at a laboratory temperature of 24° C. were outlined at noon of one day with a pen, using photographer's opaque. By noon of the following day, when the flask was photographed (FIG. 2), the rhizomorphs had finished growing across the bottom of the flask and turned up along one side, making an average advance of 2.5 cm. during the 24-hour period. In a similar flask culture of *A. mellea* growing under the same conditions thalluslike rhizomorphs ranging from ½ to 1 inch wide grew in length from 1 to 1.5 cm. during the same period. Both were growing on potato-dextrose-maltose agar with sawdust and cubes of oak wood. As a general rule, *C. tabescens* grew much more rapidly than *A. mellea* under the same conditions in all cases where comparisons were made.

MYCELIAL GROWTH

The growth of the surface mycelium in both fungi was quite variable in regard to rate, character, and color, even in a series of isolations from one plant or a series of subcultures from a given isolate. It usually developed very slowly regardless of whether rhizomorphs formed or not and frequently no appreciable growth of mycelium developed until after a fairly extensive development of rhizomorphs. In most cases mycelial growth was fairly luxuriant after it developed but in other cases the growth was very meager and test tube cultures frequently dried up before the surface of the agar slant became covered.

The initial growth from the inoculum in *C. tabescens* started as a white, velvety mycelium but subsequent growth was closely appressed to the surface of the agar, forming a compact mat. The color changes varied considerably according to the luxuriance of growth and age of the culture. The white mycelium first formed soon turned tawny and then pale tan to light brown in the majority of moderately young cultures. As the cultures became older the mycelium gradually darkened and the older parts usu-

ally became cinnamon-brown to dark reddish-brown or sepia-colored. In actively growing cultures the marginal growth frequently remained white while the older portion of the mycelial mat became progressively darker toward the center, sometimes with a slight zonate effect. In slow-growing cultures or old ones, however, there was a less striking contrast of colors and the white marginal growth may darken similarly to the color of the older portion. The older part of the mycelial mat became thickened irregularly and sometimes with a floccose, nodular, or tufted effect. The margin of the mycelial mat usually terminated abruptly but tended to become effused in slow-growing cultures. Sometimes, especially in very slow-growing cultures, simply a thin, pulverulent growth developed over the surface of the agar. Minute drops of brownish liquid frequently exuded from the mycelial mat.

In both fungi, shortly after the tips of the rhizomorphs protruded through the surface of the agar a white, appressed mycelial growth began to spread from them. This mycelial growth gradually became denser and thicker and later darkened to match the color of the older portion of the mycelial mat that developed from the point of inoculation. In this way, particularly in flask cultures of these fungi, new areas of mycelial growth may develop at several points on the surface of the agar in advance of the slow-growing mycelium developing from the point of inoculation, later coalescing with it. In both fungi also, when the rhizomorphs at the bottoms of test tubes became exposed by shrinkage of the agar away from the walls, they developed a white, downy growth of mycelium (FIG. 3, A).

In *A. mellea* the growth of the surface mycellium was similar to that of *C. tabescens* in most respects but differed in others. The initial growth from the inoculum was a white, velvety mycelium but subsequent growth as a rule was less compact and more wooly than in *C. tabescens* and soon became light tan, which was the prevailing color in the majority of cultures. With age, however, the mycelium usually became reddish-brown to sepia-colored. Moderately young cultures of the two fungi so closely resemble one another that they did not appear distinguishable as a rule on the basis of the color of the surface mycelium but *A. mellea* was

characterized by a more tufted and more floccose type of growth and this afforded the most striking visual means of distinction. With age, the mycelial mat also became thickened and so tough that it was difficult to make transfers without tearing up the cultures.

In test tube cultures of *C. tabescens* from 2 to 4 weeks old the rhizomorphs occasionally developed a halo-effect which, when examined with a hand lens by transmitted light, was seen to be due to a dense but delicate growth of hyphae radiating at right angles from the rhizomorphs. This halo-effect began just back of the growing tips of the rhizomorphs and gradually became broader with increased distance from the ends, until attaining a length of about 5 mm., measured radially from the rhizomorph. The effect

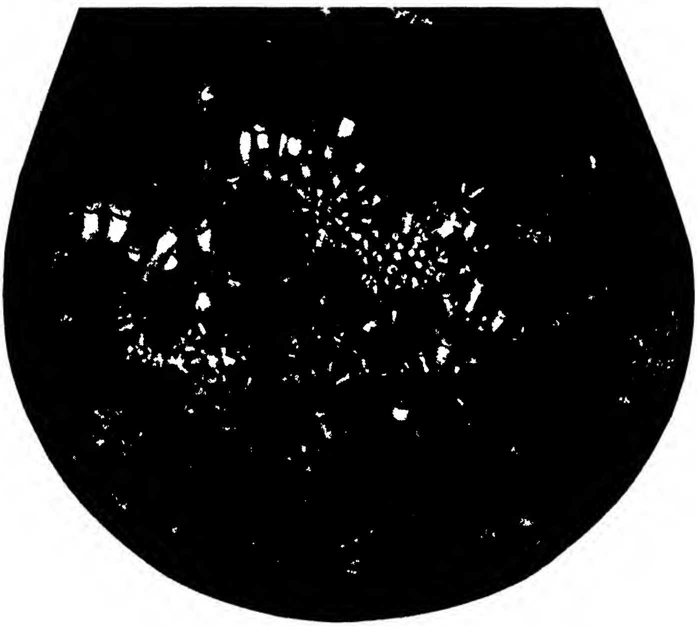

FIG. 4. Large number of buttons of *C. tabescens* developed in 500 cc. flask 3⅝ months after inoculating with isolation from sweet acacia (*Acacia farnesiana* Willd.).

is similar to the root-hair development on a radish seedling except that the radiating hyphae were much more minute and dense in comparison. In cultures of *C. tabescens* where only a series of

numerous, short rhizomorphs developed, a dense growth of hyphae has been observed occupying the upper portions of tube cultures, giving them a distinctly cloudy effect, especially when examined by transmitted light. A similar development of hyphae radiating from the rhizomorphs has been observed occasionally in test tube cultures of *A. mellea.*

In transferring cultures of both fungi to flasks it was noted repeatedly that where the inoculum was moved around the surface of the agar in placing it, growth of the fungi frequently developed simultaneously from numerous points. This suggests the possibility of secondary spore formation.

LUMINESCENCE

It has long been known that the mycelium of *A. mellea* is characterized by exhibiting the phenomenon of luminescence or noctilucence. It has been established that the luminescence of the mycelium is influenced by external conditions as well as by its age and conditions of growth. The addition of certain chemicals has been shown to increase luminescence, while others, such as anesthetics which interfere with protoplasmic activity, may reduce or entirely inhibit the capacity for luminescence. Reitsma (11) found that the percentage of cultures showing luminescence varied on different media and that on cherry agar it was limited to the points of the aerial rhizomorphs. Lisi (8) reported that 9 of a selected group of 10 morphologically distinct variants of *A. mellea* studied by him exhibited luminescence under the test conditions but not all in the same degree.

The various isolates of *A. mellea* cultured by the writer have been examined on numerous occasions in comparison with those of *C. tabescens,* which is not known to exhibit luminescence. All actively growing cultures of *A. mellea,* regardless of the source, have agreed in exhibiting luminescence, though in some it was developed but weakly. In all cases the luminescence was confined to the surface mycelium and young aerial rhizomorphs, none being apparent in the submerged rhizomorphs. The entire mycelial mat on the surface of the agar rarely glowed equally throughout, the luminescence usually being stronger at some points than

at others. As the cultures became old and developed a hard, brittle crust the capacity for luminescence diminished or was lost entirely.

On the other hand, pure cultures of *C. tabescens* growing on the same media and under the same conditions have consistently failed to show any evidence of luminescence, though cultures of it and *A. mellea* have been examined together repeatedly in complete darkness. After the lapse of a few minutes to allow the eyes to adapt themselves to the darkness the cultures of *A. mellea,* that have been examined on various occasions, have, with few exceptions, glowed like live coals, while those of *C. tabescens* did not glow at all. Labeled cultures of the two fungi mixed in the dark room could be separated with unerring accuracy on the basis of the presence or absence of luminescence, except for those occasional instances where cultures of *A. mellea* fail to exhibit luminescence. This distinction alone ordinarily will prove sufficient to separate these two closely related fungi in pure culture. It should be borne in mind, however, that cultures of *A. mellea* exhibit luminescence most strongly when young and growing actively and least so when they become old and inactive.

The exhibition of luminescence by the mycelial sheets developed between the bark and the wood and within the inner layers of bark in freshly dug specimens of roots of plants attacked by mushroom root rot, however, while indicative, does not necessarily constitute proof that *A. mellea* is involved. In a few instances Florida specimens that exhibited distinctly luminescent mycelium when examined in the dark, have yielded *C. tabescens* upon culturing and the pure cultures obtained in such cases have consistently failed to exhibit any evidence of luminescence. The same situation was true of the several specimens of mushroom root rot collected at Auburn and Opelika, Alabama. The luminescence of the mycelium in specimens of *Clitocybe* root rot as it occurs in nature appears to be exceptional. Since the fungus after isolation in pure cultures has never exhibited any evidence whatever of luminescence, even though the mycelium occasionally did under natural conditions, it is thought that this phenomenon may at times be due to luminous bacteria associated with the root-rot fungus.

SPOROPHORE PRODUCTION

One of the most striking characteristics of *C. tabescens* is the readiness with which it fruits in culture. Not infrequently the original isolations in small test tubes have developed miniature clusters of mushrooms that matured and shed basidiospores. Fruiting of this fungus usually is obtained readily in large test tube or flask cultures. Some isolates fruit with unusual readiness and others more tardily. As reported by the writer (12), it appears to make no difference in the growth and fruiting of the fungus whether the cultures are started from basidiospores or mycelial transfers. In cultures started from basidiospores it is not unusual for the fungus to produce sporophores and cast spore prints in from 35 to 45 days and this has been accomplished in several cases in one month's time. It is rather amazing that a gill fungus can be carried through its life cycle, with a very limited development of mycelium and rhizomorphs, within such a short time. However, *Lentinus lepideus* Fr., *L. tigrinus* Bull. ex Fr., *Schizophyllum commune* Fr. all develop sporophores in a rather short time in cultures.

Fruiting in test tube cultures, both in the case of original isolations and mycelial transfers from stock cultures, has been accomplished in even less time. An original isolate from Jerusalem-thorn (*Parkinsonia aculeata* L.) developed sporophores that matured and shed basidiospores at the end of 25 days. The same occurred in transfers from isolates from Botree fig (*Ficus religiosa* L.), poinsettia (*Euphorbia pulcherrima* Willd.) and Surinam-cherry (*Eugenia uniflora* L.) at the end of 26, 28, and 29 days, respectively. An even more striking case of precocity of sporophore development was observed in a series of 20 isolates, made in 18 mm. test tubes, from scrub hickory (*Carya floridana* Sarg.) during the winter when growth was greatly delayed by low room temperature. In each of 5 tubes with very scant or no development of rhizomorphs, clusters of small mushrooms formed from the initial mycelial growth before it had begun to spread over the surface of the agar. In two cultures a sporophore matured sufficiently to shed spores in a minimum period of 24 days. In flask cultures, where there is a much greater opportunity for the growth

of mycelium and rhizomorphs, a much longer period usually is required for fruiting. However, when fructification occurs in such cases it is on a much larger scale.

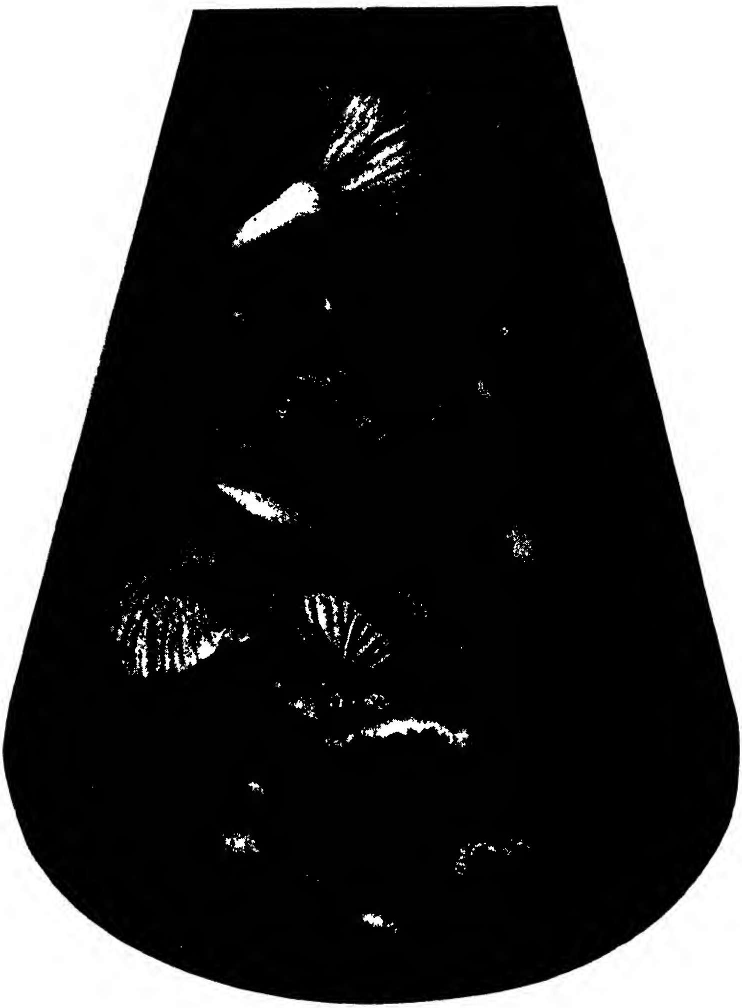

FIG. 5. Culture of *C. tabescens* shown in figure 4, photographed 5 days later to show unusually large number of mature sporophores.

When *C. tabescens* gets ready to fruit a group of little hornlike processes develops at some point on the surface of the mycelial mat and these are the primordia of the cluster of mushrooms. In test

tube cultures usually only a single cluster develops, while in flask cultures from one to several may develop. These enlarge rapidly and soon differentiate into buttons with distinct caps and stems (FIG. 4). In test tube cultures, where there is very little room for development, usually one or a very few of the sporophores that may differentiate in the cluster continue to grow and the rest abort. In some cases all may dry up before maturing. Even in flask cultures, especially when several clusters of embryonic sporophores are differentiated, most of them abort and only a few continue developing. Even when several mushrooms develop for a time, further growth usually is centered in one or two. The largest specimen grown in a 500 ml. Erlenmeyer flask was a single sporophore that prevailed over the others. This developed a cap 7.5 cm. broad and a stem 1.5 cm. in diameter at the largest point but attained this unusual size only by the stem curving so that the cap grew sidewise near the top of the flask. Figure 5 shows an unusual number of sporophores maturing in a flask of this size with none being particularly large. In the great number of cultures that have fruited over a period of several years the sporophores invariably have been typical of *Clitocybe,* with the gills distinctly decurrent on the stem and no sign of an annulus. In both test tube and flask cultures the initial production of sporophores may be followed shortly or within a few weeks by the production of new ones (FIG. 3, A) if the cultures do not become unduly desiccated.

In the writer's cultural work with *C. tabescens* over a period of several years two instances have been noted where sporophores differentiated from the ends of rhizomorphs and both occurred in cultures in test tubes. The origin of sporophores in this manner appears to be very rare for this fungus, though it has been illustrated frequently for *A. mellea.* The first case noted was in a transfer from an isolate from a cherimoya (*Annona cherimola* Mill.). Three rhizomorphs that grew upward through the surface of the agar slant developed 5 miniature mushroom buttons, with two on the upper rhizomorph, two on the next lower one, and one on the lowest one. One of the pair on the end of the middle rhizomorph developed into a mushroom about ½ inch in diameter and shed a good spore print. The other case was an original isolate from a painted copperleaf (*Acalypha Wilkesiana* var. *A. mar-*

ginata Hort.) bush. A cluster of miniature mushrooms developed from the end of a rhizomorph that grew upward near the top of the agar slant. The upper two of these mushrooms matured and shed basidiospores in a little more than a month from the time of making the isolation (FIG. 3, B).

Of the numerous isolates of *A. mellea* from a wide variety of sources cultured along with *C. tabescens* by the writer over a period of several years, none has shown the slightest indication of fruiting, not even on bread. The experience of Richards (**18**) with respect to fructification in these fungi was similar. She readily obtained sporophores from the single isolate of *C. tabescens* which she had but was unsuccessful in getting any of the 6 isolates of *A. mellea* to fruit. Reitsma, who secured and illustrated fruiting in *A. mellea,* mentioned (**11**, p. 505) that it was generally stated that it grew best on bread. In a series of cultures of this fungus made by Lisi (**8**) to encourage sporophore production, only one variant responded of the 10 morphologically distinct ones that were studied. The great readiness with which *C. tabescens* fruits in culture and the total lack of fruiting of *A. mellea* when grown on the same media and under the same conditions clearly demonstrate that these fungi, though very similar in many respects, are quite distinct.

COMPARATIVE INFLUENCE OF TEMPERATURE ON GROWTH

A study was started in June 1937 to determine the comparative influence of 8 different temperatures on the growth of *C. tabescens* and *A. mellea.* In this experiment there were used as sources of inoculum 8 isolates of *C. tabescens* from different hosts from various parts of Florida, 3 of *A. mellea* comprising isolates from California, Pennsylvania, and Wisconsin, and 1 of its tropical analogue, *A. fuscipes,* isolated by Gadd from tea (*Camellia sinensis*). A series of 16 transfers was made from each of these cultures to 1 × 8-inch test tube slants of potato-dextrose-maltose agar, which has proved an ideal nutrient medium for the growth of these fungi. This provided duplicate transfers from each stock culture at each of the 8 temperatures used. These transfers were held until it was apparent that growth was starting in all. They were then placed

in their respective refrigerators and incubators and held for 30 days. These temperatures ranged from 12.3° to 40.1° C., based on the average of the daily readings for the period.

C. tabescens grew at all temperatures used from 12.3° to 35.8° but did not grow at 40.1° C. It made the best and about equally good growth of mycelium and rhizomorphs at 24.7°, 29.0°, and 31.6°. The growth of this fungus was very good at 21.7°, fair at 14.2°, slight to fair at 12.3°, and slight at 35.8° C.

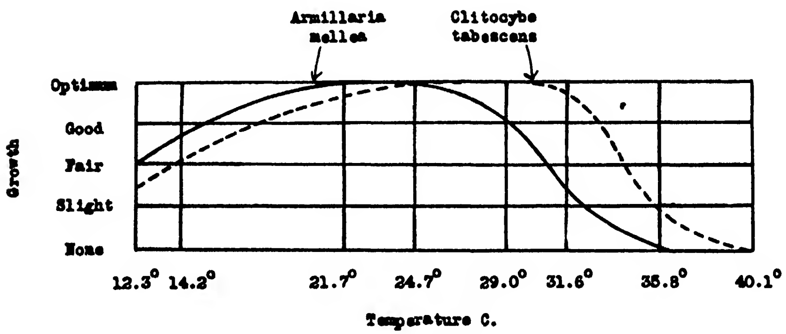

FIG. 6. Graphic comparison of growth of *C. tabescens* and *A. mellea* at different temperatures, showing the distinctly higher range of the former for optimum growth.

A. mellea and its tropical analogue, *A. fuscipes*, behaved essentially the same and grew at all temperatures used from 12.3° to 35.8° but did not grow at 40.1°. They made the best growth of mycelium and rhizomorphs at 21.7° and 24.7°. The growth of these fungi was very good at 14.2°, good at 29.0°, fair at 12.3°, fair to slight at 31.6°, and slight to none at 35.8°. This comparison, which has been expressed graphically in figure 6, shows that *C. tabescens* has a distinctly higher temperature range for optimum growth than *A. mellea.* Exposure to the high temperature of 40.1° C. for 30 days proved lethal to both fungi, as previously reported (**14**), since not a single culture of either revived after being removed from the incubator. The investigations by Wolpert (**21**) and Reitsma (**11**) showed that 15°, and 15–19°, respectively, were less suitable for growth of *A. mellea* than 25° C., which both considered the optimum. Recently, Benton and Ehrlich (**2**), working with 10 isolates of this fungus from western white pine (*Pinus*

monticola), concluded that the optimum temperature for growth in plate cultures lies between 19° and 25° and probably is between 21° and 25° C., the latter range agreeing with the results obtained by the writer.

The apparent absence of *A. mellea* in central and southern Florida and its infrequent occurrence in the northern part of the State in contrast with the prevalence of *C. tabescens* throughout the State as a whole appears to be attributable to the different temperature relations of these two root-rot fungi for growth. *A. mellea* has been found to occur, chiefly saprophytically, in areas of hammock forest around Gainesville but apparently fruits but rarely. It fruited with unusual abundance, however, during the fall and winter of 1937, the prolonged cool weather of the fall apparently sufficing to induce the development of sporophores. In general, *C. tabescens* largely replaces *A. mellea* in Florida and some of the other southeastern States.

COMPARATIVE INFLUENCE OF pH REACTION OF MEDIUM ON GROWTH

Preliminary attempts were made by the writer (**14**, **15**) to determine the effect of the pH reaction of the media on the growth of *C. tabescens* and *A. mellea*. In June 1937, 84 1 × 8-inch test tubes of potato-dextrose-maltose agar with a pH reaction of 6.3 after sterilization were divided into lots of 14 and these lots adjusted by titration to give pH reactions of 3.9, 5.3, 6.3, 7.0, 7.6, and 8.7, respectively. Preliminary tests were run on extra tubes to determine the number of drops of HCl or KOH necessary to add to each tube to adjust to these respective pH values. Each lot of tubes was titrated as necessary, after warming to liquefy, and the tubes agitated to mix thoroughly before cooling. Four isolates of *C. tabescens,* from different hosts from various parts of Florida, and 3 of *A. mellea,* comprising isolates from California, Pennsylvania, and Wisconsin, were used as sources of inoculum. Transfers in duplicate were made from each stock culture for each pH value. These were held for 30 days at room temperatures ranging from 28 to 30° C.

The 4 isolates of *C. tabescens* averaged about equally good growth of mycelium and rhizomorphs at all reactions but there was less tendency to develop sporophores on the alkaline side of the

range. The 3 isolates of *A. mellea* averaged equally good growth of mycelium and rhizomorphs at all reactions from pH 3.9 through 6.3 but produced a progressively decreasing amount of growth beginning with pH 7.0, which is in close agreement with the results secured for the latter fungus by Wolpert (21).

In September 1939, a set of 50 ml. Erlenmeyer flasks of potato-dextrose-maltose agar with peptone were divided into lots of 10 and these lots were adjusted to pH reactions of 4, 5, 6, 7, and 8, respectively, prior to sterilization. In checking after sterilization these reactions were found to have changed to pH 4.2, 5.2, 5.6, 6.4, and 7.1, respectively. A set of 5 flasks with agar of each of these pH values was inoculated with pure cultures of *C. tabescens* and a duplicate set with *A. mellea*, thus making 25 cultures in each series. These flasks were held at room temperatures ranging from 24 to 27° C.

The rapidity of mycelial growth and rhizomorph development varied greatly in the different transfers of both series at the start, irrespective of the reaction of the medium. While all transfers of each fungus were made from a single culture, greater variation occurred in growth from the different transfers than was manifest at the different pH reactions. In the *C. tabescens* series growth at pH 4.2 was retarded at first but equaled that in the other flasks by the end of 4 weeks, when, with the exception of one flask at pH 5.6, the surface of the agar in practically all was covered with mycelial growth and the bottoms with rhizomorphs extending up the sides toward the surface of the agar. In the *A. mellea* series growth at pH 4.2, with the exception of two flasks, also was somewhat retarded in general at first. Growth in this series was less vigorous than in the *Clitocybe* series. At the end of 6 weeks it was apparent that all lots of both fungi averaged approximately the same growth regardless of the reaction of the medium. At the end of this period, when the growth of the cultures began to be checked by desiccation, the majority of the flasks in the *Clitocybe* series had developed masses of embryonic sporophores, whereas none of the flasks in the *Armillaria* series showed any evidence of fruiting.

The foregoing experiments have yielded no particularly striking results with respect to the optimum reaction of the medium for the

growth of either of these fungi, other than to indicate that it apparently is not particularly significant within certain limits and that both have a wide pH range on the acid side of the scale. In his study of *A. mellea*, Wolpert (21) found that the pH limits and optimum pH zone varied with the temperature and the medium. At 25° C. in Richard's solution growth was inhibited by pH 2.9 and 6.9 and the optimum occurred at pH 4.9, while in bacto-peptone solution growth was inhibited by pH 2.0 and 7.8 and the optimum occurred at 3.8. With both media, however, he secured a fairly good growth over a relatively wide pH range but this fell rapidly to zero as the neutral point was reached or passed. Reitsma (11) secured the maximum growth at pH 5.1 in his series of cultures at the optimum temperature of 25° C. His results also showed good growth over a considerable pH range and he stated that at 25° C. the optimum lay between pH 4.6 and 6.4. In his study of the relation of growth of *A. mellea* to the pH concentration of liquid media 2 relatively slow-growing variants of the 10 morphologically distinct ones studied by Lisi (8) showed no conspicuous growth optimum while with others the optimum ranged between pH 4.0 to 6.0. He found that the variants altered the final pH of the nutrient solution in different degrees, some towards the alkaline side and others toward the acid side. However, the amount and the direction of change in the final pH were not correlated with the amount of growth. Benton and Ehrlich (2) found two optima for the growth of their isolates of *A. mellea* at 25° C. on malt agar, namely pH 4.5 and 5.5. A pH of 5.0 proved to be the most favorable, and a pH of 3.0 the least favorable, for development of rhizomorphs. Judging by these results, it does not appear that the growth of either of these fungi is sufficiently limited by the pH reaction of the medium to offer any practical application from the standpoint of control measures.

SUMMARY

The taxonomy of *Clitocybe tabescens* is discussed with reference to the assumption by some mycologists not especially familiar with the plant, that it is merely an exannulate form of *Armillaria mellea*. The importance of the isolation of the fungus, in the absence of

sporophores, in the diagnosis of the root rots caused by these respective fungi, especially in regions where both may occur, is indicated.

The root rots caused by these closely related fungi have been found to agree with respect to the symptoms exhibited by attacked plants, general appearance and growth of the mycelial sheets, development of xylostroma outgrowths extruded through longitudinal fissures in the bark of attacked roots, the marked predilection of the fungi for oak roots, and their ability to develop either parasitically or saprophytically. The root rot caused by *C. tabescens* differs, however, in the absence of the black, rounded or flattened, cortical and hypogeal, stringlike rhizomorphs, the perforate character of the younger mycelial sheets and their less fan-shaped type of development at the advancing margins.

Cultural studies of a large number of isolates of these fungi have shown further striking differences, though there was considerable variation in growth and rhizomorph production, as well as in readiness of fruiting in the case of *C. tabescens,* among the different isolates. Considerable variation also occurred frequently in series of transfers from individual isolates in both species. *C. tabescens* consistently made a more rapid growth than *A. mellea.* It usually fruited with great readiness, whereas *A. mellea* never exhibited the slightest tendency to fruit. The aerial rhizomorphs of *C. tabescens* are short and relatively blunt at the tips and remain light-colored; those of *A. mellea* usually are long and needle-shaped and become dark reddish-brown to blackish.

Pure cultures of *C. tabescens* have consistently failed to show luminescence, whereas those of *A. mellea* usually exhibited it more or less strongly, at least when young and growing actively. Moreover, *C. tabescens* has been found to have a distinctly higher temperature range for optimum growth than *A. mellea* (25–30° C. as against 21–25° C.). This appears to account for it largely replacing the latter fungus in Florida and other southeastern States. A temperature of 36° C. was close to the upper limit for growth of both fungi, especially *A. mellea,* and 40° C., maintained for a month, proved lethal to both.

Both fungi in cultures on potato-dextrose-maltose agar exhibited a wide pH range on the acid side of the scale, starting with pH

3.9 in one series and pH 4.2 in another. *C. tabescens* grew well in general at all reactions up to pH 7.1 in one series and pH 8.7 in another but fructification was inhibited on alkaline media, while *A. mellea* appeared to be distinctly intolerant of alkaline conditions and growth diminished rapidly after the neutral point was reached. However, it does not appear that the growth of either fungus is sufficiently limited by the pH reaction of the medium to offer any practicable application from the standpoint of control measures.

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AN ANALYSIS OF THE MECHANISM OF BUDDING IN YEASTS AND SOME OBSERVATIONS ON THE STRUCTURE OF THE YEAST CELL[1]

CARL C. LINDEGREN

(WITH 20 FIGURES)

Budding of yeasts is an extraordinarily unique method of cell division and heretofore no one has elucidated the mechanism. The present study reveals that budding is the direct result of the extension of a tube from the vacuole to a point on the cell wall where a very tiny protuberance is formed on the outer surface of the cell into which the vacuole-tube passes and in which it enlarges to form the bud-vacuole. The following description of the structure of the yeast cell will serve to orient the reader.

THE STRUCTURE OF THE YEAST CELL

The structure of the cell of *Saccharomyces cerevisiae* has been the subject of much dispute, but Wager and Peniston's observations are, in my opinion, the most complete that have been made and my own observations follow theirs closely. Their "text-figure," which summarizes their findings, is reproduced herewith (FIG. 1). Table I lists the designations which they gave the different organelles along with the name applied to the same structures by Guillermond, Janssens and Leblanc, and myself. Wager and Peniston's interpretation was limited by contemporary concepts of cell structure, but their drawings reveal an organization easily understandable in terms of modern concepts of the nucleus. They show that the yeast nucleus has a structure similar to that described by Harper (**1905**) for the Ascomycete, *Phyllactinia*. Attached to one side of the nuclear vacuole is a smaller body which

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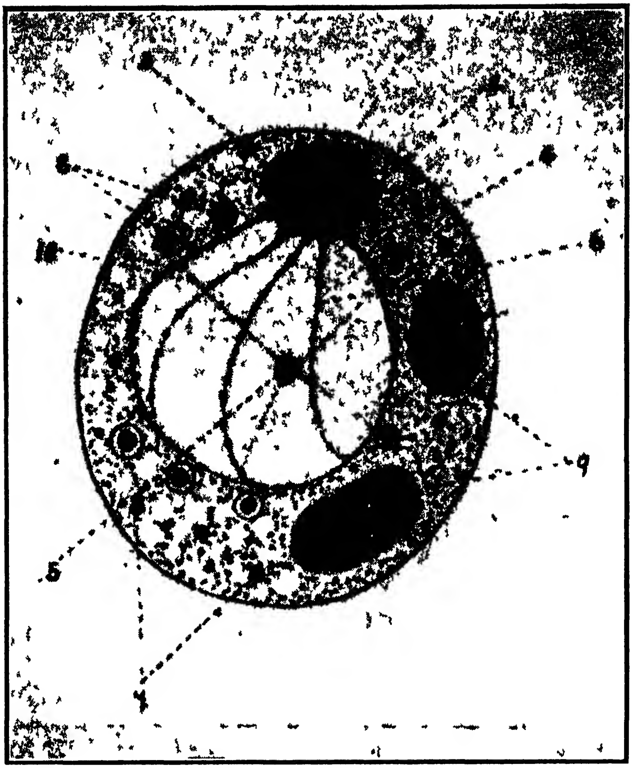

FIG. 1. Yeast cell from Wager and Penniston.

TABLE I

NAMES OF ORGANELLES IN FIGURE 1 BY DIFFERENT AUTHORS

Wager and Peniston	Guilliermond	Janssens and Leblanc	Lindegren
1. Nucleolus	Nucleus	Nucleolus	Centriole
2. Peripheral layer of chromatin			
3. Chromatin patch on one side of nucleolus			
4. Nuclear vacuole	Vacuole	Nucleus	Nuclear vacuole
5. Central volutin granule in the vacuole			Nucleolus
6. Chromatin network			Chromosomes with chromomeres
7. Granules of fatty substance			
8. Volutin granules			Volutin
9. Glycogen vacuoles			Glycogen
10. Delicate suspending threads for the central volutin granule			

is not ordinarily visible in the living cell and which other workers, notably Guillermond (1910), called the nucleus. This structure was called the nucleolus by Wager and Peniston; it corresponds to the centriole in *Phyllactinia* and it has many characteristics of the fungal centriole. The nucleolus is inside the nuclear vacuole and Wager and Peniston called it the "central volutin granule in the vacuole." Wager and Peniston distinguished clearly between the volutin granules attached to the outer wall of the nuclear vacuole, and the chromatin granules (chromomeres) which are inside the nuclear vacuole and borne on chromosomal fibers according to the current conventional concept. The chromosomes are attached to the structure, which I shall call the centriole, exactly as they are in the higher ascomycetes. The large eccentric centriole with polarized chromosomes is characteristic of the fungi. Guillermond probably mistook the centriole for the nucleus because it divides at each mitosis, shows internal structure, and retains hemotoxylin rather firmly.

According to the view presented here, the nucleus is a compound structure containing the hemispherical centriole intimately attached to the nuclear vacuole. Observation of growing cells usually shows that the vacuole is flattened on one side and otherwise is almost a perfect sphere (FIG. 4). The flattened side of the nucleus is the area of attachment to the centriole. The centriole is usually not visible in unstained material but can be brought out by treatment with iodine. On one side of the centriole and about one-fifth its size in some cells, there appears near the juncture of the vacuole and the centriole, another body described by Wager and Peniston as the "chromatin patch." This structure can also be observed in some cells suspended in .01 per cent methylene blue. It stains a faint blue while the vacuole fills with pink dye (FIG. 5).

OBSERVATIONS OF THE CHROMOSOMES

A fruitful method for observing yeasts is to mount them in .01 per cent methylene blue. The dead cells and the living cells stain quite differently. At first the cytoplasm of dead cells stains a light blue. The vacuole of the dead cells later takes on a pinkish tinge and the chromosomes in the vacuole stain a light red. Even-

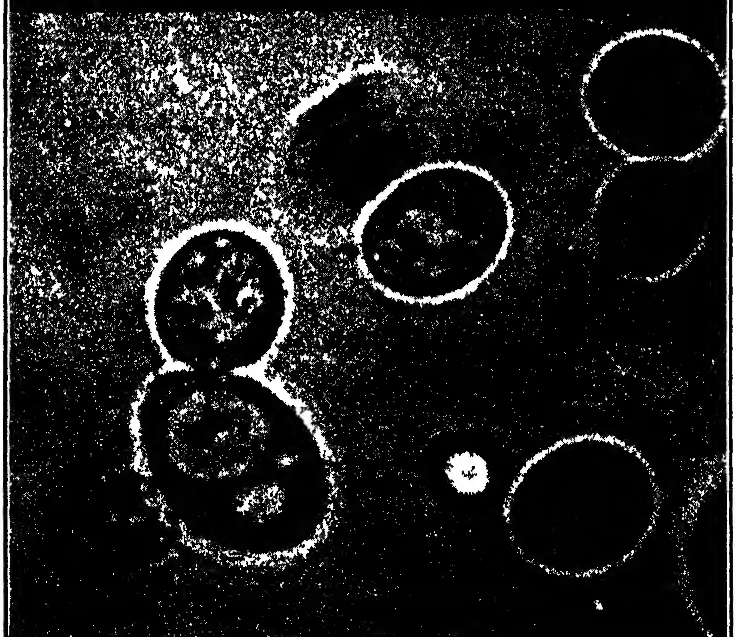

FIG. 2. Yeast Cells

FIG 3 Yeast Cells

tually the dead cells become completely over-stained with methylene blue. However, in the living cells, at the outer edge of the slide or on the border of a bubble, the chromosomes, within the nuclear vacuole, often take on a deep blue color and are clearly visible as small irregular, twisted bodies, sometimes polarized, but usually free and in rapid Brownian movement. In the dead cells the pink nuclear sap is coagulated and the chromosomes are stationary. The stain in the chromosomes of the living cells is evanescent and apparently depends upon the oxidation potential within the cell. From 10 to 20 minutes after they have taken on their intense deep blue they completely disappear under observation, presumably due to reduction of oxidized dye to the leucobase (FIG. 2, 3). This indicates that the methylene blue passes through the highly reduced cytoplasm as the leucobase and becomes oxidized on contact with the surface of the chromosome which probably does not have much reducing power. After the stain disappears it can be brought back by a second addition of the dye. Usually only one or two pairs of chromosomes stain by this method. The chromosomes appear to be paired somatically but critical observations are difficult and each chromosome might be folded back upon itself (FIG. 6, 7). Sometimes several are tangled together in an irregular mass.

On the addition of more dye, the chromosomes may reappear in the vacuole and the dye remains in them longer this time, apparently due to the diminution of the amount of reducing substance in the cytoplasm, possibly because the cells are losing some of their vitality. Sometimes the chromosomes inside the cells ball up into small, tightly-wound bodies that cease their Brownian movement and attach themselves to the inner face of the nuclear membrane. Occasionally the chromosomes seem to be polarized (FIGS. 8, 9) and I have observed the long threads retract toward a single point of attachment at the side of the nuclear vacuole (FIG. 10). The phenomenon has somewhat the appearance of a crystal becoming deliquescent. Eventually one finds either one or more large lenticular blue-black masses appressed to the inside of the nuclear vacuole. Six is the largest number which I have observed in diploid cells. If the chromosomes were paired this would represent the haploid number. In old aniline blue lacto-phenol prepa-

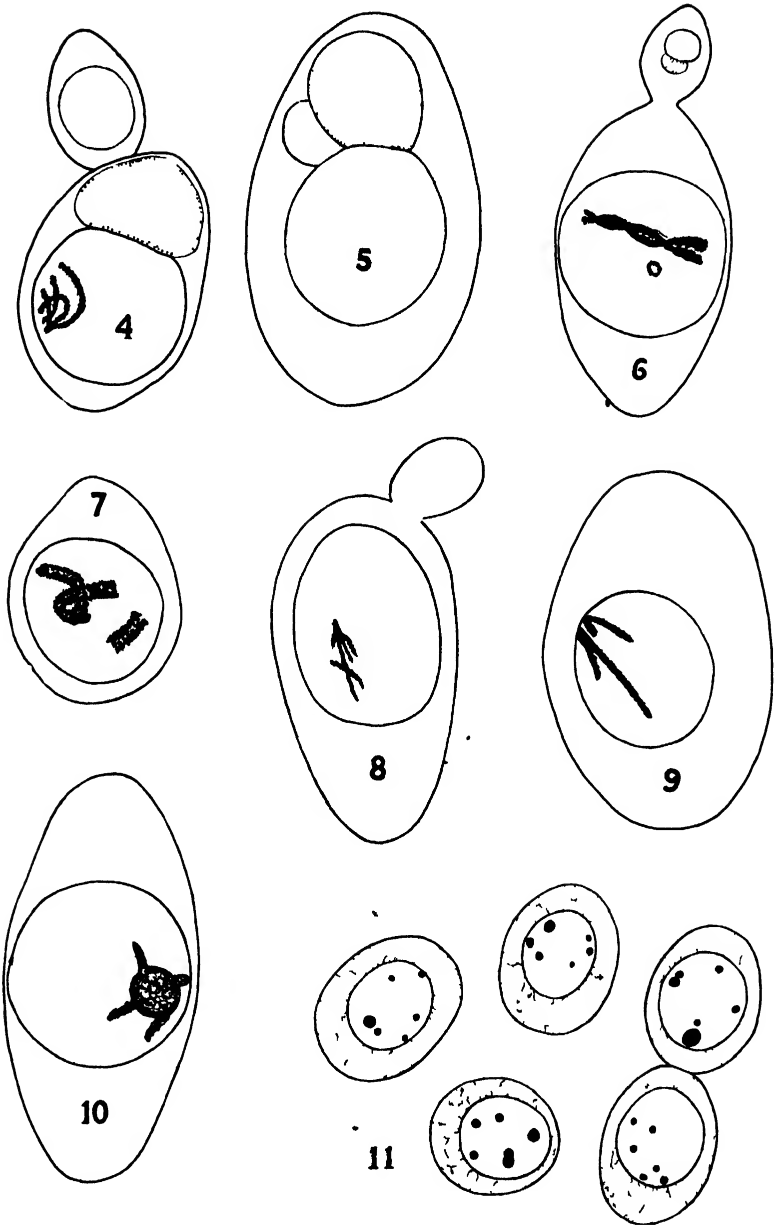

FIG. 4–10. Outline drawings of yeast cells. FIG. 11. Same showing blue staining bodies.

rations the cells contain from one to six clearly defined, light blue bodies inside the nuclear vacuole (FIG. 11) produced by the attachment of the chromosomes to the wall of the vacuole just as with methylene blue. The aniline blue stain is stable. Figure 11 is a drawing reconstructed from photographs.

MOVEMENT OF THE CHROMOSOMES IN THE VACUOLE

When a small drop of aniline blue in lacto-phenol is placed near the edge of a wet mount and allowed to diffuse between the slide and the cover slip, in some of the vacuoles one can observe long, slender, delicately beaded thread-like strands vibrating in the nucleoplasm. These structures do not take the dye but seem merely to change their refractive index (possibly due to action of the acid or the phenol) so that they become observable. Sometimes one larger, thicker strand, possibly produced by the coalescence of several strands, may be seen moving sinuously in the nuclear sap. The strands are usually polarized although this may not always be the case. Even the slender ones seem to be relatively rigid, bending something like a very slender, but rather long thin steel wire. The chromosomes in this condition are only visible momentarily and soon disappear but they resemble Wager and Peniston's figures closely enough to constitute confirmation of their observations. In the case of their preparations fixed with $HgCl_2$ and subsequently stained, the chromosomes are attached to the inner surface of the nuclear vacuole and are motionless. $HgCl_2$ apparently prevents the "balling up" of the chromosomes which occurs when living preparations are treated with methylene blue or aniline blue.

These observations indicate that the chromosomes in the living cell vibrate in the nuclear sap. After one has observed the phenomenon in cells in which the refractive index of the chromosomes makes them unmistakably visible, suggestions of the movement are visible in other yeasts such as *Torula utilis, Saccharomycodes ludwigii,* and *Schizosaccharomyces octosporus.* The motion continues after flooding with Lugol's iodine which stains the glycogen brown and often brings the chromosomes into higher relief. The vibration of the chromosomes should greatly facilitate

the exchange of materials between the nuclear sap and the cytoplasm.

While the lacto-phenol is diffusing into a wet mount some of the cells in its path reveal a large number of smaller bodies in active Brownian movement in the nucleoplasm paralleling observations which I have made on moribund yeast cells. These particles have not been identified. In some unstained yeast cells I have observed similar small bodies inside the nuclear vacuole in rapid continual motion. Their activity is strongly reminiscent of the movements of a flock of midges hanging in the summer air. The motion is too rapid to permit counting although estimates of from 30 to 60 may be made. They are all about the same size and are evenly suspended throughout the nuclear space, while the nucleolus or the "balled up" chromosomes (one cannot tell which) moves sluggishly on the floor of the nuclear vacuole in low focus. In some cells the sluggish body is not apparent. This phenomenon is observable in about 10 per cent of the cells of several special strains of *S. cerevisiae* after the cultures have been grown in broth for a few days.

Badian found that the structures, which I have called the centriolar bodies, take the Feulgen stain and this has been confirmed by Dr. Hampton Carson and Miss Lillian Nagel (unpublished, personal communication). However, chromosomes are structures which perform a specific biological function rather than specific chemical compounds and the morphological evidence described in this paper indicates to me that the general rules concerning the specificity of the Feulgen stain for chromosomes do not hold in yeasts.

THE DIVISION OF THE CENTRIOLE

Badian (1937) developed an exceedingly effective stain for bacteria and fungi. He killed the cells with osmic vapors, stained with methylene blue and destained with eosin. He studied mitosis and meiosis in *S. cerevisiae* and stated that the cells contained two chromosomes which divided by longitudinal splitting. However, his figures show that the so-called chromosomes always pull apart finally by thinning out at the middle and the final separation is by a crude transverse fission. Furthermore, he stated that the haploid

chromosomes fuse end to end to form the diplophase, rather than associating to form a pair of chromosomes according to the usual method. If his conception is correct the number of chromosomes in haplophase and in diplophase would be the same. The life cycle as described by Badian is shown in figure 12 copied from his paper.

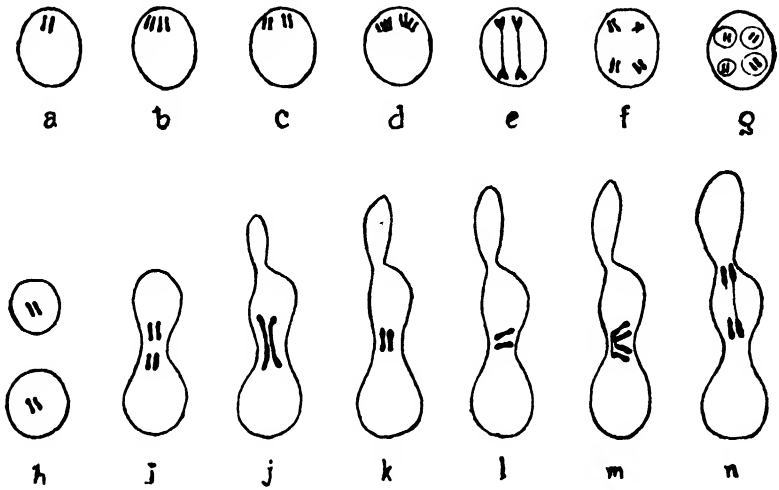

FIG. 12.

The structure which I have called the centriole contains two rod-shaped bodies which stain well with aceto-orcein and divide by a crude transverse fission. They are the only bodies in the cell which take this stain and they are undoubtedly the bodies described by Badian as the chromosomes. Badian concluded that at copulation the chromosomes fuse end to end to produce the diplophase. However the vacuoles also fuse at that time and it seems more probable that he actually observed the fusion of the rod-shaped components in the centriole rather than of the chromosomes themselves. Harper (1905) proved that fusion of the nuclei in *Phyllactinia* is initiated by contact of the centrioles, although his techniques did not reveal any internal structure in the centrioles. If the fusion of the nuclei in yeasts were initiated by end to end fusion of the centriolar bodies, the anomaly described by Badian in which a diploid chromosome is supposedly produced by the end to end fusion of two haploid chromosomes would be explained.

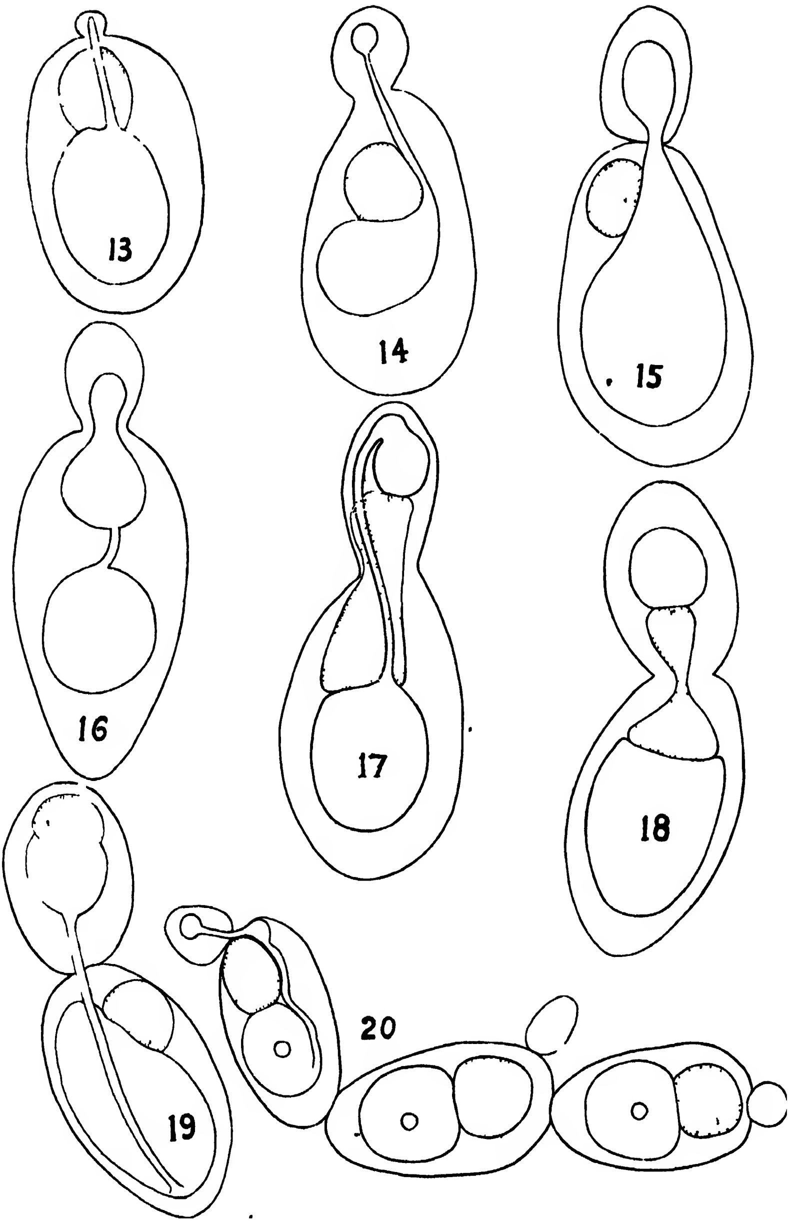

FIG. 13–20. Outline drawings of yeast cells.

BUDDING

When a yeast cell buds both the nuclear vacuole and the centriole divide. The first step is the formation of a long slender tube leading from the vacuole to the periphery of the cell (FIG. 13). This phenomenon can only be observed in cells containing enough glycogen so that the iodine stain delimits the vacuole and its tube as a clear space in the surrounding reddish brown cytoplasm. Observation is facilitated by the use of a Wratten 45 filter which converts the reddish brown color of the cytoplasm to blue-black and reduces the chromatic aberration of the lens system. The canal from the vacuole may begin any place on the surface of the vacuole, but usually appears at a point near the attachment of the vacuole and the centriole (FIG. 13, 14, 15, 17). The bud is always produced near the centriole and when the canal emerges at the opposite side of the vacuole, the long, slender channel extends all the way from the most distant part of the cell through the cytoplasm and finally produces the bud near the centriole (FIG. 19, 20). Occasionally the bud-opening is too small to permit the contents of the vacuole to enter the bud and the canal is distended at this point like the oesophagus of an ostrich swallowing an orange (FIG. 16, 20). A bulb is produced at the end of this canal to form the bud-vacuole (FIG. 14, 15, 17, 19, 20). During this period the centriole is a hemispherical solid unyielding structure that is not deformed by movements of bodies near it. After the bud-vacuole is formed the centriole divides (FIG. 17, 18, 19). Sometimes in the Lugol's solution, it is seen as two bodies which appear to divide by stretching out and thinning out at the center. After the division of the centriole is completed and the establishment of contact of bud-vacuole and bud-centriole has been attained, the interconnecting canal between the mother and the bud-vacuole disappears.

As soon as the bud approaches the size of the parent cell, the nuclear apparati in bud and mother cell reorient themselves so that the centriole in each cell is distal to the bud partition. This is easily observed in single pairs of cells and is also seen in the first two cells of the chain in figure 20.

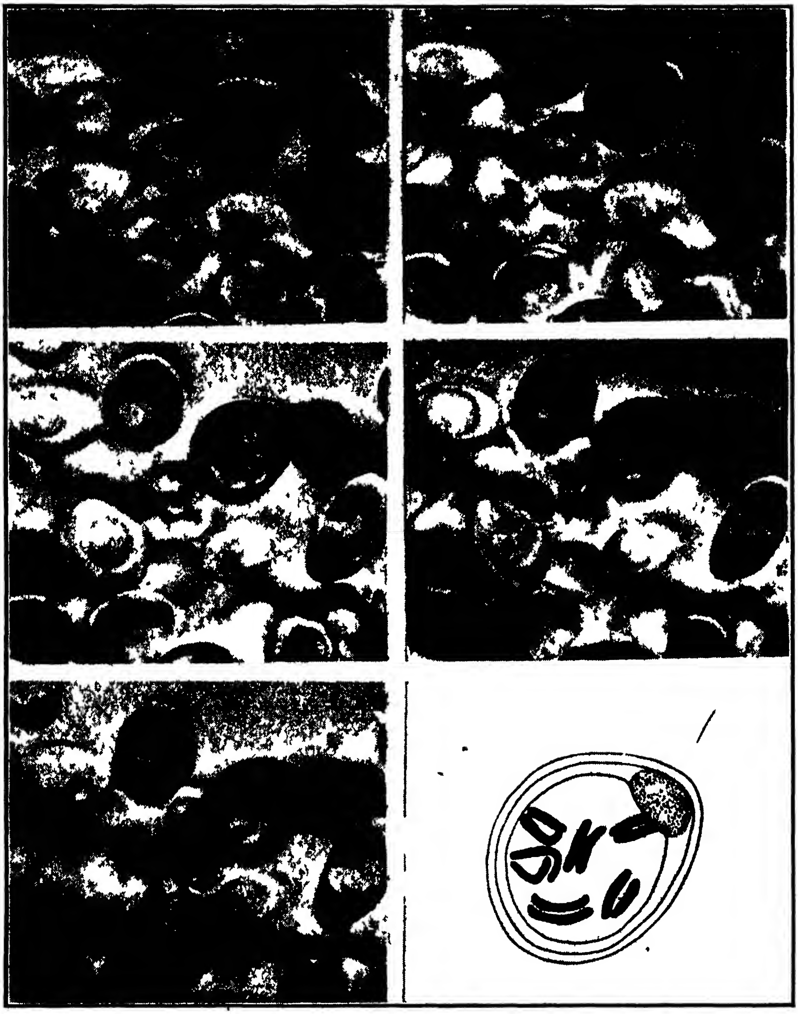

FIG 21 Yeast cells showing chromosomes

SUMMARY

The ability of yeast cells to reproduce by budding has distinguished them from other fungi as well as from other organisms and the observations presented here show that the mechanism is quite unique. The nuclear vacuole puts out a slender tube which forms a small protuberance on the cell wall and as the bud grows an en-

largement in the end of the vacuolar tube produces the bud-vacuole.

Observations on unstained cells confirm Wager and Peniston's concept of the structure of the yeast chromosomes and reveal that the polarized chromosomal threads vibrate in the nucleoplasm.

THE HENRY SHAW SCHOOL OF BOTANY,
WASHINGTON UNIVERSITY,
ST. LOUIS, MISSOURI

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EXPLANATIONS OF FIGURES

FIG. 1. A drawing copied from Wager and Peniston, showing their interpretation of the structure of the yeast cell.

FIG. 2, 3. Two photographs taken within a few minutes of each other, one of which shows chromosomes in the vacuole in Brownian movement. The other, taken a few minutes later, shows how the dye has faded from the chromosomes.

FIG. 4, 5, 6, 7, 8, 9, 10, and 13 through 20. Outline drawings showing the vacuole and its processes in yeast cells. The centriole, when visible, is stippled. Discussion in text.

FIG. 11. Drawings showing the blue bodies inside the nuclear vacuole found in aniline blue lacto-phenol preparations. These drawings have been reconstructed from photographs taken through several foci. The cells showing the largest number of chromosomes were chosen.

FIG. 12. Yeast life cycle as described by Badian. This figure is copied from his paper showing spore formation from the diploid cell (a-g), and the fusion of two haploid cells to reconstitute the diploid (h, i, j). Arguments are presented in the present paper suggesting that these bodies are not the chromosomes as Badian had thought, but components of the centriole.

POSTSCRIPT

An especially clear toluidine blue preparation has confirmed the above suggestion that yeasts contain 12 somatically paired chromosomes. The five photographs shown in figure 21 were taken

through five different optical levels of a cell. The first shows a pair of central chromosomes, the second and third a pair at the extreme right of the cell, and the fourth shows four other pairs of chromosomes, with single mates revealed in the fifth. The drawing is a reconstruction of the entire cell with the centriole stippled in at the position where distortion of the vacuole and the cell wall has revealed its presence.

A NEW SPECIES OF LYSURUS

W. C. Coker

(with 6 figures)

In June 1945 there appeared in a "soil table" in the botanical laboratory of Clemson College, S. C., an ample colony of a very small phalloid. The table contained local garden soil mixed with imported sphagnum of origin now unknown. The material as brought to us consisted of 16 expanded plants and 9 buttons, mostly single, a few with volvas superficially fused. We describe it as follows.

Lysurus pusillus sp. nov.

Mature plant 1–1.5 (2.2) cm. high, color of volva and stipe dull white, gleba dark brown with a faint tint of olive, odor fetid but not strong; button subspherical, 4–6 mm. thick, largely covered with soil particles, attached at base by one to several strong white, ropy strands which soon branch into a delicate complex, or by more delicate and numerous filaments. Stipe 7–18 mm. high, 2.5–3.5 mm. thick, terete, attenuated below, surface delicately wrinkled, hollow, wall about ⅔ mm. thick, very uneven within, the flesh chambered with a single row of irregular cavities, not constricted above, where it divides into 3–4 (5) bluntly pyramidal, entirely separate, but closely folded, vertical or irregular curved arms which may or may not form a regularly pointed apex, the arms bluntly ridged on the back, the ridge with a shallow central furrow that broadens below and is continuous with the stem; arm surface entirely covered both within and without, except for the ridge furrow, and a little of the base on the inner surface, with irregular, horizontal wrinkles which support the gleba, these folds and gleba running over the apex of the stipe between the bases of the arms so as to connect them. Gleba dark brown with a faint tint of olive, firm, smooth, the tramal cavities as usual very small and irregular. Basidia multi-

spored (up to 8 seen), long, narrow, tapering below and narrowed above; spores elliptic, 1.8–2 × 3.7–4.4 μ.

FIG. 1–6. *Lysurus pusillus.*

Receptaculo parvo, 1–2.2 cm. alto; volva subglobosa, pallida; stipite alba, 7–18 mm. longa, tereti, apice non dilatato et diviso in lobos 3–5, lanceolatos,

subacutos, rugosos, apicibus non connexis; gleba ante liquefactionem lobos includente et plane celante; sporis ellipticis, 3.7–4.4 μ longis.

Distinguished by small size, lack of color and arms which are free at the tips and, on first expanding, completely embedded in the gleba.

Types are placed in the Herbaria of the University of North Carolina, Clemson College, and Harvard University.

Single or caespitose in garden soil mixed with sphagnum, Clemson College, S. C. D. B. Rosekrans and A. E. Prince, Coll. June 14, 1945.

This is one of the smallest known phalloids. It seems nearest *Anthurus cruciatus* (Lepr. & Mont.) Ed. Fischer which also is pallid and about the same size, but if that is correctly described and drawn it could not be the same plant. The gleba is figured as a ball embraced by the exposed arms, which indicates the genus *Anthurus,* where it is placed by Fischer. (See Montaine: Ann. Sci. Natur. 3rd Series. Vol. **4**: 360. *Pl. 14, fig. 1.* 1845, as *Aserophallus cruciatus,* and Fischer: Natur. Pflanzenfam. Band **7a**: p. 92, *fig. 66 H.* 1933.) It was found on rotten wood in French Guiana about 100 years ago and so far as we know has not been reported since. Lloyd says the types are preserved in Paris. (Syn. Known Phalloids, p. 40, *fig. 44.* 1909.)

UNIVERSITY OF NORTH CAROLINA,
CHAPEL HILL, NORTH CAROLINA

EXPLANATION OF FIGURES

FIGS. 1 and 2. Three plants, one the largest found. Natural size.

FIG. 3. Basidia and spores. × 1080.

FIG. 4. Young plant, with volva torn open, and with stipe not fully extended. The gleba has been washed off to show the arms. × 6.5.

FIG. 5. Tip of an arm, showing inner side. × 9/100.

FIG. 6. The same showing outer side and central furrow. × 9/100.

Figure 3 is by the writer, others by Alleda Burlage.

FURTHER REMARKS ON MYCOGENETIC TERMINOLOGY

(CONCLUSION)

B. O. DODGE

(WITH 9 FIGURES)

Zickler's diagrams (**1934**, p. 585) are confusing because of the typographical errors in two of his figures. These diagrams are reproduced here in our figures 1, 2, with the errors corrected. The symbols ⚥ and ♂ have been added by the writer. Zickler holds that the reaction group factors *A* and *a* represent sterility factors and not factors which govern the development of ascogonia and spermogonia. In any event, whatever the *A* and *a* reaction groups do represent, every one will agree that they are not tied up with the production of "sex" organs in this or similar cases. The symbol ♂ means that the race, as cultured, produced many spermatia, although in this paper Zickler (**1934**) admits that some incipient ascocarps are occasionally produced by his *lan* races. ". . . die *lan* Stämme keine oder nur ganz vereinzelte weibliche Geschlechtorgane ausbilden." The *bulb* races form both ascogonia and spermatia and so are represented by the symbol ⚥.

Comparing figures 1 and 2 below we see, as Zickler pointed out, that he did not have in *Bombardia* the tetrapolar type of reaction such as exists in certain mushrooms (FIG. 2). But, he suggests, p. 585, if a *bulb* race *should* lose completely its power to form spermogonia, then he *would* have an example of tetrapolarity. So, in a later paper (**1937**), and without reporting any additional culture experiments as a basis for his statement, he says there *are* *bulb* races that do not produce spermogonia. Figure 3 would then picture the situation in such a case. The writer believes, judging from the results of his breeding experiments with *Neurospora* and especially with *Pleurage anserina* (**1935**), that "♀" races of *Bombardia* could be developed. One wonders why Zickler did not analyze the progeny of such a cross as shown in this figure 3.

Hansen and Snyder (**1943**) reporting their culture work with *Hypomyces solani* f. *cucurbitae* present in their diagrams, p. 421, essentially the same condition as that described by Zickler (**1904**) for *Bombardia*. They do not, however, indicate that they had races of the reaction group *a* that are female, ♀. Their theory of the "dual phenomenon" which now calls for a *mutation* from C to M or from hermaphroditic ⚥, to male, ♂, would probably rule out such a possibility in their *Hypomyces*. Furthermore, their definition of sex must be interpreted, having in mind their conclusion: "Any part of a living thallus, ascospores, conidia or bits of mycelium can act as the male fertilizing element." This brings up the question as to the real nature of the microconidia of *Fusarium* or, for that matter, the microconidia of any other fungus. Is any conidium to be classed as a spermatium and therefore male, ♂, if it can act as a fertilizing element? Or is a conidium a spermatium and male only when it is small? Why is it that authors discussing maleness and femaleness in the fungi so often avoid referring to the situation in species of *Neurospora*? Are the tertiary conidia ot *Neurospora* spermatia? They are just as small as are the bona-fide spermatia and they function in the same ways.

Zickler (**1934**, p. 583) proved very clearly that the wall of the ascocarp is neither a hybrid structure nor a mixture of tissues to which both of the haploid parental races contributed. The mycelium and primordia of race *viridis* are greenish. Race *rubiginosa* has reddish-brown mycelia and primordia, and race *lactea* is whitish. Regardless of the source (color) of the race from which the spermatia were obtained for spermatization the color of the mature perithecia was always the same as was that of the mycelium and primordia spermatized. Hansen and Snyder (**1943**) in their figure 2 show that the same principle holds for their *Hypomyces*.

The writer was unable to obtain from Zickler cultures of his *Bombardia* for study. That author did not carry on his genetic work to test out his ideas on sex and sterilities. The questions we want answered would include: Are there factors or genes for antheridia and factors for ascogonia? If so, are these allelic, and where are they located on the chromosomes and on which chromosomes? One should not resort to those hypothetical "realizers" or "determiners" unless those F and M genes are located, especially

with reference to those heritable genes governing phenotypic differentiations of "sex" cells. When a ⚥ mutates to a ♂ race in *Hypomyces* or to a female, ♀, race in *Bombardia,* what is the gene picture before and after the mutation?

Above all Lindegren (**1936**) has given us a six-point sex chromosome map for *Neurospora crassa,* a sex chromosome map based on the idea that the +/− or *A/a* relation is a sex-reaction or a mating type relation. Would it be out of place to insist that, from now on, authors in attempting to explain maleness and femaleness in the fungi give us, as Zickler, for example, has done for *Bombardia,* accurate illustrations of the structures which they classify as male or female. One wonders if Hüttig (**1935**) really expected any one who had ever studied sexual reproduction in Ascomycetes to take his illustrations of the oögonium and antheridium of *Glomerella* seriously.

Another thing, should not our future mycogeneticists volunteer to make the races on which they have based important conclusions available to others for study in case it seems desirable to have one's work confirmed by an independent worker? It would throw much light on the nature of reproduction and inheritance in the Ascomycetes if some one would prove absolutely that there exist or could be developed races of *Bombardia, Neurospora, Pleurage* and *Hypomyces,* for example, that are stable "male" races as well as stable "female" races. Then show where on the chromatids the factor complexes for ascogonia and spermatia are located and how they are or are not linked with the +/− or the *A/a* mating type factors.

In suggesting such experimental studies the writer is not attempting to be facetious. On the contrary, he believes that the development of morphological structures such as ascogonia and spermogonia is governed by heritable genes or gene complexes. Zickler as noted above would have us believe that his ⚥ race *bulb* mutates to a ♀ *bulb* race, while Hansen and Snyder (**1943**) appear to believe the reverse mutation ⚥ to ♂, or C to M, is the rule. They do not discuss either Zickler's work on *Bombardia* or for that matter the work of Lindegren and others on *Neurospora.* After having studied sexual reproduction in *Ascobolus carbonarius* and *A. magnificus* and having seen those striking and highly differentiated ascogonia and antheridia it would be impossible for the

writer to lose interest or faith in the part such structures play in reproduction and inheritance.

Figures 4–9, following Zickler's scheme, may help to visualize "sexual reproduction" in these heterothallic fungi from two quite different standpoints. First, maleness and femaleness always imply phenotypic morphological sex-cell differentiations. Second, the more fundamental principle of sexuality is that which applies to the simplest as well as to the most complex forms. This implies physiological genotypic sex-reactions or mating type, +/− or *A/a*, segregations. We see this best exemplified in the heterothallic yeasts, smuts, mushrooms and Mucorales. It also operates in exactly the same way in *Ascobolus, Bombardia* and *Neurospora,* for example, where differentiation of "sex organs" occurs sooner or later. In figures 1–9 solid lines indicate positive results or production of ascocarps, dotted lines indicate negative results.

The mycelium of *Neurospora tetrasperma* is normally mictohaplontic or heterocaryotic. Each of the two components when separated normally can be induced to develop ascogonia and spermatia, so that from this standpoint the *A* and *a* component mycelia are both hermaphroditic, ⚥, just as in the normal heterocaryotic mycelium itself. If we grow these two components together mixed in tube cultures the results are depicted in figure 4. In *Spirogyra* the cell that sends its nucleus out through the conjugation tube is, to the differentiationists, male, ♂; the cell in which the zygospore is matured is female, ♀, as indicated in figure 5. If we now grow our *A* and *a* component races in a plate culture (FIG. 6), the perithecial distribution pattern is such that, on the *Spirogyra* basis, the *a* race is male, ♂, and the *A* race is female, ♀. Figure 7 brings out the relationship.

Gelasinospora tetrasperma is much like *Neurospora tetrasperma,* except that in the former all races, both mictohaplontic and unisexual, are female, ♀, spermatia are not as yet known. For the perithecial distribution patterns which are the same for the two species, see Dodge, 1931, pl. 7, fig. 17 and 1935, pl. 39. Figure 8 diagrams the situation in the *Gelasinospora* from the viewpoint of morphological differentiation of sex organs, while figure 9 follows in line with sex differentiation based on the criteria for maleness and femaleness in *Spirogyra.*

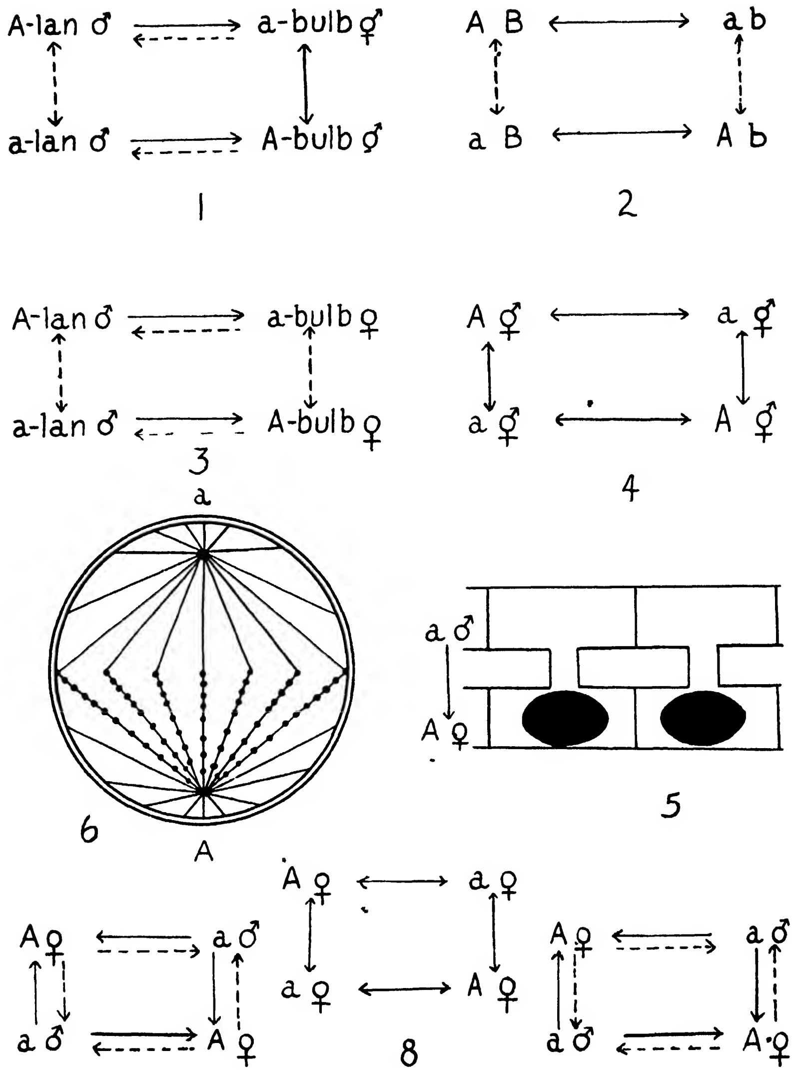

FIG. 1. *Bombardia.* Diagram, adapted from Zickler (**1934**), showing the reactions between races *A* and *a* as related to morphological differentiations of ascogonia and spermatia by the races involved; 2. Tetrapolar sexuality in a mushroom; 3. Reactions between mutant races of *Bombardia;* 4. *Neurospora tetrasperma.* All normal races potentially hermaphroditic, sex-reactions independent of sex-cell differentiations; 5. Male ♂ and female ♀ cells

If the reader is somewhat confused as to the meaning of the diagrams in terms of sex, he should remember that his confusion may be due largely to our use of the symbols for male, female and hermaphrodite, and to the bringing into the discussion morphological differentiations which are often entirely secondary and not primary factors which determine whether or not two races of a heterothallic species will react sexually in reproduction. If one is carrying out genetic studies for the purpose of locating those genes or factor complexes which govern the development of ascogonia and antheridia, and for finding out how such genes are linked and how they are segregated at meiosis, then the symbols would certainly serve a very useful purpose. In such cases we must have, as noted previously, adequate illustrations of those structures which the author would call male or female. One source of confusion has always been the insistence of an author that if a certain structure *acts* as male it is, in fact, male; and so with female.

Zickler (**1937**, b) evidently had not seen the paper on *Pleurage anserina* (Dodge, **1936**). Races No. 5, 9 and 19 never produce spermatia. Figure 1, B, in that paper, illustrates how a race which produced no spermatia yet could "act as male" by supplying nuclei which migrate over to the receptive race. These striking perithecial distribution patterns and the variability with which races produce or fail to produce spermatia and perithecial primordia indicate that those who will undertake a thorough genetic study of this species will be well rewarded because abundant evidence can be unearthed to support almost any theory of sexuality. *Neurospora tetrasperma* is still better because its spermatia, "male, ♂, sex organs," germinate and go on to make normal mycelia. One thing stands out above all else, namely, regardless of where one finds the latter species, Surinam, Australia, Puerto Rico, Texas or the Canal

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of a heterothallic species of *Spirogyra*. We are assured that a cell is male if its nucleus migrates over, and the cell receiving this nucleus and forming the zygospore is female; 6. Diagram of perithecial distribution pattern in plate culture, the sexuality, male ♂ and female ♀, determined by the direction of nuclear migration and production of fertile ascocarps; 7. Diagram of a plate culture following Zickler's schemes; 8. *Gelasinospora tetrasperma*. All races morphologically female, but sexual reproduction is the result of reaction between sex-reaction or mating types *A* and *a;* 9. Diagram interpreting perithecial distribution pattern in terms of sex in *Spirogyra*.

Zone, the species is facultatively heterothallic, and the component races in every case fall into the same two sex-reaction groups, +/— or *A/a*. This reaction is not only intraspecific but also *interspecific*. True heterothallism in the fungi and algae is of the same nature as it is in Blakeslee's Mucoraceae. It is primarily based on the principle of segregation of genes or gene complexes which regulate the events leading up to and including the sexual fusion of nuclei to form zygotes.

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NOTES AND BRIEF ARTICLES

ANNOUNCEMENT

Mycologia's New Editor-in-Chief

When Mycologia was adopted as the official organ of the newly formed Mycological Society of America, two editorial positions were provided for, an Editor-in-Chief, to be selected by the Editorial Board from among their number to take care of the editorial work of the journal, and a Managing-Editor, appointed by the New York Botanical Gardens to look after its financial interests. Up to the present time, the two positions have been handled as one. It seems expedient now to separate the duties of the two offices. This is a rather delicate surgical operation, but it is hoped the patient will survive and suffer no serious shock.

The Editorial Board has approved the appointment of Dr. Alexander H. Smith of the University of Michigan as Editor-in-Chief, his duties to be taken over in January 1946. Dr. Smith seems to be well qualified both as to training and location in one of the outstanding mycological centers of America. All manuscript for publication in Mycologia should be sent to Dr. Smith.

The writer will continue to act as Managing-Editor for a time at least. I am sure the Mycological Society will give Dr. Smith the loyal coöperation and support which I have had during my term of office. Our best wishes are extended to the new Editor-in-Chief.—Fred J. Seaver.

A Manual of Soil Fungi [1]

The above named volume by Joseph C. Gilman has recently appeared. As stated by the author, this is largely a compilation of material previously published in scattered literature for which there has been much demand. To supply the demand its publication in book form seems warranted.

[1] The Collegiate Press Inc., Ames, Iowa.

The fungi are taken up essentially in the order in which they are treated by Engler and Prantl in "Die natürlichen Pflanzenfamilien" with some variation to fit more modern treatments.

It is needless to say that such a compilation cannot be in any sense complete but lists those forms which the author himself has actually encountered. The book is intended to be used as a guide to others who may wish to continue the study of the microörganisms of the soil and their functions which have not been fully appreciated.—FRED J. SEAVER.

WOLF'S AQUATIC OÖMYCETES OF WISCONSIN [1]

The introduction presents a summary of the more important taxonomic works on the Saprolegniaceae. This is followed by descriptions of the orders, families, genera, and species of Oömycetes found in Wisconsin by the author and by former workers. Twenty-two genera with fifty-five species are included. The descriptions are particularly well written, and the illustrations, some original and others copied, will be helpful to subsequent students in identifying the Oömycetes.—JOHN N. COUCH.

FISTULINA IN FLORIDA

I never expected to record the Beefsteak Mushroom, *Fistulina hepatica* Fr., for Florida, but Dr. G. F. Weber collected it on Aug. 19, 1945, near Keystone Heights, on the road to Camp Blanding. It grew in sandy soil in a thicket of scrubby live-oaks, doubtless attached to buried wood. The spores were pure hyaline under the microscope when fresh, smooth, ovoid, uniguttulate, about 4–5 × 3 μ. The best treatment of this genus is probably in Atkinson's "Mushrooms," pp. 186, 187, where colored illustrations are given of both *F. hepatica* and *F. pallida*.—W. A. MURRILL.

ABORTIPORUS SUBABORTIVUS MURR. IS VALID

In "Lloydia" for June, 1945, Dr. Rolf Singer makes *Abortiporus subabortivus* Murr. a synonym of *Daedalea philippinensis* Pat. A glance at the differences given below will show that the

[1] Wolf, F. T. The Aquatic Oomycetes of Wisconsin, Pt. I. 64 pp., 6 pls. The University of Wisconsin Press, Madison, 1944.

two are distinct. In Patouillard's species the pileus is azonate, cream to fuscous; stipe 8 cm. long, glabrous, appearing varnished; spores 7–9 μ long, echinulate. In my species the pileus is zonate, rosy-isabelline; stipe 4–6 cm. long, not appearing varnished, its surface spongy and finely tomentose; spores 5–6 μ long, minutely roughened. See Bull. Torr. **65**: 655. 1938 for complete description.—W. A. MURRILL.

BOLETUS TABACINUS Peck

In Mycologia **36**: 362. 1944, Dr. Singer states that my *B. pisciodorus* is not distinct from the above but he probably did not have the two types together on the same table as I have now. In *B. tabacinus* the tubes are collapsed and umbrinous, the spores a dark yellowish-brown; in *B. pisciodorus* the tubes are firm, not at all collapsed, larger and fulvous, the spores hyaline under the microscope. Age may make some difference but hardly that much. Peck's species grew in red clay on the bank of a roadside ditch; mine under hickories, oaks, etc. in moderately moist sandy soil among grasses and weeds. The latter has a decided fishy odor at maturity and in drying. Perhaps someone in Alabama can find more of Peck's species and note its odor and the color of its fresh spores. I am indebted to Dr. House for the loan of the type and to Dr. Seaver for specimens collected in Alabama by Earle on Sept. 6, 1899.—W. A. MURRILL.

KARLING'S SIMPLE HOLOCARPIC BIFLAGELLATE PHYCOMYCETES [1]

This book is the second of a series of lectures presented to graduate and research students of mycology at Columbia University on the origin, development, phylogeny, and evolution of the lower organisms. The first book described the Plasmodiophorales, and the present one includes the biflagellate Phycomycetes exclusive of the Leptomitales, Saprolegniales, and Peronosporales. This admittedly heterogeneous assemblage includes about eighty species, twenty genera, and five families, for which the author suggests the group name of Holobiflagellomycetes.

[1] Karling, J. S. Simple Holocarpic Biflagellate Phycomycetes. 123 double column pages, and 25 plates. Published by the author, New York City, 1942.

The introductory chapter reviews the historical background justifying the separation of the simple biflagellate species from the Chytridiales. A separate chapter is devoted to each of the five families, Woroninaceae, Ectrogellaceae, Olpidiopsidaceae, Sirolpidiaceae, and Lagenidiaceae, in which the family characteristics are fully discussed and all the genera and species are illustrated and described, including even the ones whose phylogenetic positions are doubtful or which are inadequately known, a practice which will be very helpful to future workers. However, these chapters are by no means solely taxonomic, for the morphological, cytological, and other literature is also completely reviewed and summarized. Chapter seven is devoted to an impartial discussion of the relationships of the Holobiflagellomycetes to the lower forms, as *Proteomyxa,* on the one hand, and the higher forms, as the Saprolegniales, on the other. The author's viewpoint is expressed as follows: "Present day evidence suggests very strongly that most of these Holobiflagellomycetes are either remotely or closely related to the higher Phycomycetes. However, it is not clearly evident whether they are primitive or reduced and degenerate. . . ." The final chapter is a valuable summary of hosts and bibliography.

The book contains some typographical errors most of which, however, are trivial and detract only slightly from the beautifully smooth and easy-flowing style. In Chapter 2, Zopf's important paper on *Woronina glomerata* is omitted from the bibliography. On page 116 the reference to this paper is given twice: "heft" 2 is given when it should be heft 4, and in the first reference the name of the journal is wrong. The illustrations are well executed, but the author omitted the magnifications of all the figures and the source and explanations of some are left out.

This book, by one of the world's authorities on the lower fungi and related organisms, will be of great service to students and investigators in mycology and hydrobiology.—JOHN N. COUCH.

A CHANGE IN GENERIC NAME

In Mycology **31**: 371. 1945, the generic name *Whetzelia* was proposed by the writer to include the much confused species

Urocystis Waldsteiniae Peck or *Ustilago Waldsteiniae* Pazsche. Since publication it has been discovered that in 1934, Chardon and Toro had already used the generic name *Whetzelia* for a new genus of the Sphaeriales in Venezuela containing one species, *Whetzelia venequelensis,* Chardon and Toro. (See Myc. Expl. of Venezuela —Monographs of the University of Puerto Rico Ser. B. **2**: 185–186. 1934. This situation requires a renaming of the smut genus. The name **Ustacystis** is therefore suggested. In a letter to the writer concerning this species some years ago, Dr. Whetzel casually suggested the appropriateness of this name. The name indicates the complex character of the species in that the germination is characteristic of a Ustilago while morphologically it is somewhat characteristic of a Urocystis. The previously published description of *Whetzelia Waldsteiniae* applies to the new names **Ustacystis Waldsteiniae** (Peck) Zundel.—GEORGE L. ZUNDEL.

THE PRODUCTION OF A PENICILLIN-LIKE FACTOR BY DERMATOPHYTES

The possible production of penicillin by organisms other than those of the *Penicillium notatum-P. chrysogenum* group is a matter of considerable scientific interest. Among the numerous surveys of various fungi for antibiotic activity is a recent report on the dermatophytes by Peck and Hewitt (Peck, Samuel M., and William L. Hewitt. The production of an antibiotic substance similar to penicillin by pathogenic fungi (dermatophytes). Public Health Reports (U. S. P. H. S.) **60**: (6) 148–153, Feb. 9, 1945).

A strain of *Trichophyton mentagrophytes,* when grown on a modified Sabouraud's broth at 30° C., was found to produce a substance antibiotic to *Staphylococcus aureus.* The antibiotic activity of the substrate appeared on the third or fourth day, increased to the ninth to fourteenth day, and then levelled off; the maximum activity obtained was equivalent to two units of sodium penicillin per cc. The addition of yeast extract, magnesium, calcium, potassium, iron, lactose, thiourea, or ascorbic acid to the culture medium did not increase the yield. The organism failed to

grow upon the corn-steep medium routinely used in commercial penicillin production with *P. notatum*, but when one per cent neopeptone was added to this substrate *T. mentagrophytes* produced an antibiotic factor in a concentration equivalent to 8–10 units per cc. of sodium penicillin. Strains of *T. violaceum, T. tonsurans* and *Epidermophyton floccosum* also were found to produce small amounts of an antibiotic factor, while strains of *T. rubrum, Microsporum canis*, and *M. audouini* did not. The antibiotic factor produced by dermatophytes was found to be similar to penicillin in respect to its enhanced production on media containing corn-steep liquor, its spectrum of activity and behavior toward penicillin-resistant organisms, its sensitivity to pH and temperature, and its destruction by clarase.—FRED WOLF.

NEW BOLATACEAE FROM FLORIDA (a preliminary communication)

While a full monographic treatment of the Boletaceae of Florida, including notes on extralimital species, is in preparation, it is felt that a preliminary account containing the new forms observed and studied there by the writer, during his tenure of a Fellowship from the Guggenheim Memorial Foundation (1942–43), would be helpful for those who are interested in the floristic or taxonomic problems involved. The total number of species observed is 53, of which 7 species and 12 varieties and subspecies are here described as new. Five new combinations are proposed.

Boletus auripes Peck var. **aureissimus** (Murr.) Sing. comb. nov. = *Ceriomyces aureissimus* Murr.

Boletus griseus Frost subsp. **Pini-caribaeae** Sing. ssp. nov. A typo sporis paulum majoribus et habitatione sub *Pinibus caribaeis* differt. Coral Gables, Fla.

Boletus Weberi Sing. sp. nov. Pileo argillaceo-avellaneo, areolato-squamuloso, sicco, 65 mm. lato; hymenophoro luteo, poris rubris ornato, circa stipitem depresso, immutabili, poris amplis; sporis 9–15.3 × 4–5.5 μ, melleis, levibus; cystidiis 14–60 × 4–6.5 μ; hyphis fibulis destitutis; sporis in cumulo olivaceo-brunneis; tramate typi *Boletorum;* stipite ad apicem rubro, basin versus olivaceo-griseolo, subfibrilloso-subpunctulato, deorsum distincte squamuloso, solido, 53 × 17 mm.; carne pallide flava, subinodora. Sub *Pinibus australibus* ad terram in Gainesville, Fla.

Boletus granulosiceps Sing. sp. nov. Pileo brunneo vel fusco, subtiliter granuloso vel velutino, 30–65 mm. lato; elementis hymenialibus in cuticula trichodermiali nullis; hymenophoro flavidulo, circa stipitem subdepresso,

poris laesis caerulescentibus, amplis; sporis 8.8–13 × 4.5–5.5 μ, levibus; cystidiis 23–56 × 6.8–11 μ, subulatis vel fusoideis; tramate typico *Boletorum;* hyphis haud fibuligeris; stipite brunneo vel sepia-granuloso vel furfuraceo, ceterum pallidiore, subaequali, 30–50 × 6–8 mm.; tomento myceliali sordide pallido vel albido; carne stipitis brunneola vel pallida, saepe caerulescente, pilei pallide flava vel pallide aurantiaca, caerulescente. In dumetis tropicalibus aestate, prope et in Miami, Fla.

Boletus subsolitarius Sing. sp. nov. Pileo cinnamomeo-fusco, ferrugineo-brunneo, atrofusco, subtiliter granuloso-furfuraceo vel subtomentoso et plerumque strato velutino tenuissimo flavo obtecto, 32–38 mm. lato; margine hymenio tecto; hymenophoro citrino vel aurato, circa stipitem subdepresso, immutabili, poris latis; sporis 8–13.5 × 4.7–5.5 μ, olivaceo-brunneis in cumulo; cystidiis fusoideis; tramate typico *Boletorum;* stipite flavido vel albidulo, apice furfuraceo, 33–38 × 11–12 mm.; mycelio tomentum luteum efformante; carne albida vel flavida, immutabili. In dumetis tropicalibus prope Miami, Fla.

Boletus rubellus Krombh. subsp. **consobrinus** Sing. ssp. nov. Pileo carmineo-subpurpureo vel olivaceo; sporis 9.2–11 × 4.7–5.4 μ; odore nauseoso vel subnullo; stipite appresse fibrilloso; mycelio laete viridi-flavo. In dumetis tropicalibus prope Miami, Fla.

Boletus rubellus Krombh. subsp. **dumetorum** Sing. ssp. nov. Pileo roseo-testaceo; stipite flocculoso-squamuloso vel subfurfuraceo; mycelio basali flavo; carne rarissime caerulescente sed superficiebus saepe tactu caerulescentibus. In dumetis tropicalibus prope Miami, Fla.

Boletus rubellus Krombh. subsp. **caribaeus** Sing. ssp. nov. Pileo testaceo, ad marginem fortiter tomentoso; sporis (9.5)–10–14.2–(16.3) × 4.2–6.5 μ; stipite flocculoso-punctulato vel subfurfuraceo, 58–67 × 10–25 mm.; mycelio sordido; carne caerulescente, inodora. Locis apricis sub *Pinibus caribaeis* prope Miami, Fla.

Boletus rubellus Krombh. subsp. **bicoloroides** Sing. ssp. nov. Pileo rubro, carmineo-rubro, partim brunnescente vel isabellascente, minute areolato-subgranuloso vel rimuloso-subtessellato, non viscido, 24–52 mm. lato; stipite carmineo-purpurascente, ad apicem flavo vel flavido, subglabro, sublevi, 28–64 × 5–12 mm.; mycelio cremeo-albida; carne caerulescente. Ad terram sub arboribus frondosis in Alachua Co., Fla.

Boletus austrinus Sing. sp. nov. Pileo brunneo-lilacino, tomentoso, 38–50 mm. lato; tubulis flavis, poris rubris vel intense aurantiacis; sporis 10.5–12.2 × 4.8–5.5 μ; tramate typico *Boletorum;* hyphis haud fibuligeris; stipite ad apicem flavo, purpureo-brunneo vel rubido-vinaceo flocculis furfuraceis causa, ad basin conspicue olivaceo-strigoso; 38–40 × 10–12 mm.; carne flava, fortiter caerulescente, miti. Sub quercubus prope Miami, Fla.

Boletus hypocarycinus Sing. sp. nov. A *B. subvelutipede* stipite albido (nec luteolo), rubro-punctulato vel rubro-lineato (nec reticulato), sublevi (nec flocculoso) et tomento strigoso basis destituto differt. Ad terram sub *Quercu virginiana* prope Gainesville, Fla.

Boletus miniatoölivaceus Frost var. **subluridus** (Murr.) Sing. comb. nov. = *Suillellus subluridus* Murr.

Boletus rubricitrinus (Murr.) Murr. var. **Fairchildianus** Sing. A typo poris rubris recedit. Fairchild Tropical Garden prope Miami, Fla.

Boletus Frostii Peck subsp. **floridanus** Sing. ssp. nov. A typo pileo roseo-purpurascente-testaceo (nec carmineo), tomentoso (nec glabro), minus viscido stipiteque normaliter reticulato (nec alveolato) differt. Sub quercubus in Gainesville atque prope Sebring, Fla.

Tylopilus minor Sing. sp. nov. A *T. felleo* statura minore, graciliore stipiteque pallidiore, saepius levi vel subtiliter tantum reticulato nec non habitatione in dumetis ("hammocks") frondosis differt. Kelley's Hammock prope Gainesville, Fla.

Tylopilus tabacinus (Peck) Sing. var. **amarus** Sing. var. nov. A typo pileo subpallidiore, glabriore et imprimis sapore amaro differt; cum typo rarius, Gainesville, Fla.

Tylopilus tabacinus (Peck) Sing. var. **dubius** Sing. var. nov. A typo pileo dilutius colorato, reticulatione apicis stipitis indistinctiore differt; cum typo rarius. Gainesville, Fla.

Tylopilus peralbidus (Snell & Beardsl.) Murr. var. **rhodoconius** Sing. var. nov. A typo sporis in cumulo roseolis differt. Gainesville, Fla.

Leccinum subglabripes (Peck) Sing. comb. nov. = *Boletus subglabripes* Peck.

Leccinum subglabripes (Peck) Sing. var. **corrugatoides** Sing. var. nov. A typo pileo dilute brunneolo-olivaceo et fortiter corrugato differt. Prope Gainesville, Fla.

Leccinum rugosiceps (Peck) Sing. comb. nov. = *Boletus rugosiceps* Peck.

Leccinum albellum (Peck) Sing. comb. nov. = *Boletus albellus* Peck.

Leccinum chalybaeum Sing. sp. nov. A *L. scabro* pileo partim chalybaeotincto et carne ardesiaco-purpurascente, dein nigrescente differt; a *L. albello* pilei superficie viscida et epithelio destituta ac saepe colore differt. Cum quercubus variis in hortis et in dumetis frondosis nec non in pinetis (cum *Quercus minima*). Prope Gainesville, Fla.—

ROLF SINGER.

MYCOLOGICAL SOCIETY OF AMERICA

DIRECTORY—SUPPLEMENT—1945

New Members

ALEXANDER, DOROTHY FENNELL, Junior Microbiologist, *Fermentation Division, N. R. R. L., 1218 Main St., Peoria, Ill.*

BERNHARDT, DR. ERNST, Assistant, *Department of Dermatology of the Beth Israel Hospital and of the Boston City Hospital, 370 Commonwealth Ave., Boston 15, Mass.*

BONNER, JOHN TYLER, *Aero Medical Laboratory, Wright Field, Dayton, Ohio.*

BRASFIELD, T. W. N., *2616 N. W. 30, Oklahoma City 7, Okla.*

BROOKS, TRAVIS EPPS, *1209 Ohio St., Lawrence, Kansas.*

BROWN, ARCHIBALD MOFFAT, *Dominion Laboratory of Plant Pathology, University of Manitoba, Fort Garry, Winnipeg, Canada.*

CLARK, LILY HERLINDA, Assistant, *Botany Department, U. C. L. A., 1961 Lovelace Ave., Los Angeles 7, Cal.*

CRANDALL, BOWEN S., Pathologist, *Office of Foreign Agricultural Relations, USDA*, Station Pathologist, *EEA de Tingo Maria. Estacion Experimental Agricola de Tingo Maria, Tingo Maria, Peru, S. A.*

DUCHARME, ERNEST PETER, Research Assistant, *Department of Plant Pathology, University Farm, St. Paul 8, Minn.*

DULANEY, EUGENE LAMBERT, Fellow, *Department of Botany, University of Wisconsin, Madison 6, Wisconsin.*

ECKERT, THEODORE E., *247 Brown Ave., Hempstead, L. I., N. Y.*

FULMER, W. L., *505 Boylston North, Seattle, Wash.*

GORDON, FRED MORRIS, Fellow, *Department of Plant Pathology, Cornell University, Ithaca, New York.*

GRUBER, WILLIAM BILLER, *6476 S. W. Burlingame Place, Portland 1, Oregon.*

HANSON, ANNE M., Research Assistant, *173 West 76 St., New York 25.*

HILAIRE, SISTER M., *Rosary College, River Forest, Illinois.*

IMLE, DR. ERNEST P., Senior Pathologist, *U. S. Department of Agriculture Rubber Station, Turrialba, Costa Rica.*

JOFFILY, JOSÉ, *Rua Terezina No. 13 (Sta. Tereza), Rio de Janeiro, D. F., Brazil.*

JOHANSON, ALFHILD ELIZABETH, *730 Crawford Ave., New York 66.*

JOHNSON, HARRY LEWIS, Home National Bank, *Meriden, Conn.*

KORF, RICHARD, P., *Department of Plant Pathology, Cornell University, Ithaca, New York.*

LINDEGREN, DR. CARL CLARENCE, Research Professor of Botany, *Henry Shaw School of Botany, Washington University, St. Louis 5, Mo.*

MUIR, DR. ROBERT DONALD, Senior Bacteriologist, *Cheplin Laboratories, 100 Wood Ave., Syracuse, New York.*

OLSEN, KENNETH LAURANCE, Teaching Fellow in Botany, *Washington State College, 1715 C. St., Pullman, Washington.*

RADER, WM. E., Assistant, *Department of Plant Pathology, Cornell University, Ithaca, New York.*

SAKSENA, DR. RAM KUMAR, Reader in Botany, *Department of Botany, University of Allahabad, India.*

SILVEIRA, VERLANDE DUARTE, Professor de Fitopatologia, *Escola Nacional de Agronomia, Rio De Janeiro. Rua Visconde de Pirajá. 583 c-1, Ipanema. Rio de Janeiro, Brazil.*

SIMPSON, HELEN FRANCES, Biological Laboratories, *Harvard University, Divinity Ave., Cambridge 38, Mass.*

SKINNER, CHARLES EDWARD, Assistant Professor in Bacteriology, *Department of Bacteriology, University of Minnesota, Minneapolis 14, Minn.*

WOLFE, LLOYD ROCKEFELLER, President—The W. E. Long Co., Chicago. *476 Park Avenue, Glencoe, Illinois.*

ZIFFER, JACK, Head, Department of Zymomycology, *Schenley Research Institute, Inc. Lawrenceburg, Indiana.*

ZUCK, DR. ROBERT K., Assistant Plant Pathologist, *Division of Cotton, B.P.I., U. S. D. A., R. R. 1, Box 532, Berwyn, Md.*

CHANGES OF ADDRESS

Barnett, H. L., *West Virginia University, Morgantown, W. Va.*

Braun, A. J., *N. Y. State Agricultural Experiment Station, Drawer 353, Geneva N. Y.*

Chen, S. M., *Care Dr. K. W. Wagner, 105 Winona St., Northfield, Minn.*

Christenberry, G. A., *204 Oregon St., Greenville, S. C.*

Darley, E. F., *3655 Ames St., Denver 14, Col.*

Goodding, L. N., *Winslow High School, Winslow, Ariz.*

Harvey, J. V., *11 Heiskell Ct., Jeffersonville, Ind.*

Haskins, Maj. R. A., *University of Western Ontario, London, Ont.*

Howell, A., *Medical School of Virginia, Richmond, Va.*

Hillegas, A. B., *A. S. F. Regional Hospital, Ft. Benning, Ga.*

Pope, Seth, *Schenley Research Inst., Lawrenceburg, Ind.*

Springer, M. E., *Connecticut College, New London, Conn.*

MEMBERS DECEASED

CLEMENTS, FREDERIC E.
EDGECOMBE, ALBERT EDWARD
HAGELSTEIN ROBERT
WHETZEL, HERBERT HICE

FINANCIAL STATEMENT

DECEMBER 31, 1943–DECEMBER 21, 1944

Balance on hand December 31, 1943:		
Cash		$ 636.80
Government bonds		940.00
Savings account		241.31
Receipts:		
Annual dues in part 1944, 1945		1860.00
Refund checks to members, not cashed		4.00
Expenditures:		
New York Botanical Garden for Mycologia	$1220.00	
Returned checks and discounts	7.18	
Postage and envelopes	51.19	
Secretarial assistance	30.25	
Mimeographing and printing	172.50	
Refunds to members	2.50	
Union American Biological Societies	15.00	
Bank service charges	2.31	
Expense of representative to Nat. Res. Council	10.16	
Expense of secretary to Cleveland meeting	32.48	
	$1543.57	
Balance on hand December 21, 1944:		
Cash	957.23	
Government bonds	940.00	
Savings account	241.31	
	$3682.11	$3682.11

(Signed) GEORGE B. CUMMINS, *Secretary-Treasurer*

Examined and found correct:

M. F. BARRUS, *Chairman of Auditing Committee*
Jan. 3, 1945.

INDEX TO VOLUME XXXVII[1]

INDEX TO AUTHORS AND TITLES

[1] This index was prepared by Jean N. Zodda.

INDEX TO GENERA AND SPECIES

New names and the final members of new combinations are in **bold face type.** Mistakes in the spelling of scientific names encountered in the text are corrected in the index.

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